University of Alberta

THE EFFECTS OF FOREST FRAGMENTATION ON GENERALIST PREDATION ON FOREST TENT CATERPILLARS (*MALACOSOMA DISSTRIA*)

By

Margaret A. Glasgow ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Spring 2006

Library and Archives Canada

Published Heritage Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et Archives Canada

Direction du Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-494-13815-7
Our file Notre référence
ISBN: 0-494-13815-7

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

In memory of Grandma Anne

"I am a McGarry"

ABSTRACT

Predation of forest tent caterpillar pupae by generalist predators in a variably fragmented landscape was examined over a range of background forest tent caterpillar (FTC) densities. Predation of pupae was assessed over two summers in forest fragments and tracts of continuous forest, using crossed exclusion treatments of bird presence/absence and beetle presence/absence, in two regions in Alberta. Overall, generalist predators exhibit a pattern of inversely density-dependent predation, and the magnitude of predation does not differ between forest structures. Similar trends of predation were observed in treatments that excluded just beetles or just birds. Furthermore, bird and beetle predation is additive resulting in elevated levels of predation when both predators are present. Pupal parasitism however, appears to reduce bird-type predation. Although generalist predators do not appear to regulate low density populations of FTC, this study indicates that they are important sources of pupal mortality, particularly at low FTC densities, regardless of forest structure.

ACKNOWLEDGEMENTS

Thanks to my supervisory committee: Jens Roland, Susan Hannon, and Evie Merrill, as well as the external examiner, Lloyd Dosdall, for comments on the project design and guidance in the writing of the thesis. Particular thanks to Jens for the valuable input and the countless revisions of the manuscript.

Thanks also to the field assistants Dana Sjostrum, Alyson Winkelaar, and Laura Murphy for keeping me sane and focused during long days. A big thanks to my lab-mates Dave Roth and Kim Rondeau for their invaluable input, patience and support, and also their uncanny ability to distract me when I was heading down the slippery slope of thesis writing madness! A special thanks to Kim for reading, editing and commenting on my thesis manuscripts.

Thanks to staff and students at the Meanook Biological Station, in particular Cindy McCallum for helping me with the bird sampling protocols and taking me out to learn bird calls. Thanks also Tanya Hope for her bird survey "know-how" and advice. Additional thanks to Dr. George Ball, Danny Shpeley and Josh Jacobs for their help with Carabid identification at the Strickland Museum.

Funding for this research was provided by grants from the Canadian Circumpolar Institute and an NSERC operating grant to Dr. Jens Roland. Thank you to the Alberta Ministry of Sustainable Resource Development for allowing me access to sites on public lands. In addition, thanks to the Duffin Family for allowing me access to their land.

A special thanks to Dr. Bob Lamb for inspiring me to go on with my education. I wouldn't be here without his help, guidance and encouragement.

Thanks to my family and friends who were so supportive throughout this degree. Mom, thanks for believing in me!

Thanks to you all!

TABLE OF CONTENTS

Chapter 1
General Introduction
Life History..... 2
Generalist predators of tent caterpillars..... 3
Population dynamics of forest tent caterpillars..... 3
Thesis overview..... 6
Literature Cited..... 7

Chapter 2
The effects of forest fragmentation on generalist predation of forest tent caterpillars (*Malacosoma disstria* Hübner), in central Alberta, Canada.
Introduction.....12
Methods.....15
Results.....29
Discussion.....39
Literature cited.....48

Chapter 3
Bird and beetle-mediated predation rates of forest tent caterpillars (*Malacosoma disstria* Hübner) in a fragmented landscape.
Introduction.....56
Methods.....58
Results.....65
Discussion.....77
Literature cited.....87

Chapter 4
General Conclusions
Pattern of predation across the range of FTC densities.....93
Forest structure and predation.....94
Future research 95
Literature cited.....96

Appendix A 97
Literature cited.....101

Appendix B.....111

LIST OF TABLES

Page

Table 2.1. Test of fixed effects on rates of predation by generalist predators, on forest tent caterpillar pupae in, 2003 and 2004..... 30

Table 2.2. Parameter estimates of the non-linear fit of residual predation as a function of pupal density. Data are for reference trees, in 2003 and 2004 combined..... 33

Table 2.3. Effects of forest fragment characteristics on the proportion pupae consumed by generalist predators in 2003 and 2004, combined..... 35

Table 2.4. The effects of vegetation characteristics on residual mortality of forest tent caterpillar pupae..... 36

Table 3.1. Test of fixed effects on rates of predation by avian predators and beetle predators on forest tent caterpillar pupae in 2003 and 2004..... 66

Table 3.2. The effect of prey density on *bird-type* predation. Parameter estimates are obtained from linear and non-linear fit models of residual predation after controlling for forest structure and year in 2003 and 2004..... 68

Table 3.3. The effect of prey density on *beetle-type* predation. Parameter estimates are obtained from linear and non-linear fit models of residual predation after controlling for forest structure and year in 2003 and 2004..... 69

Table 3.4. Linear and non-linear effects of landscape characteristics of forest fragments on the proportion pupae consumed by bird predators (both summers combined)..... 70

Table 3.5. Linear and non-linear effects of landscape characteristics of forest fragments on the proportion pupae consumed by beetle predators (both summers combined)..... 70

Table 3.6. The effects of vegetation characteristics on residual bird predation of forest tent caterpillar pupae over two years. Residual predation was obtained from the main effects model..... 72

Table 3.7. The effects of vegetation characteristics on residual beetle predation forest tent caterpillar pupae over two summers. Residual predation was obtained from the main effects model..... 72

Table 3.6: Repeated measures analysis of the main treatment effects on predatory bird abundance in 2003 and 2004..... 73

LIST OF FIGURES

Page

Figure 2.1. Locations of experimental regions within Alberta, Canada..... 17

Figure 2.2a. Example of landscape configuration at the *Rocky* Mountain House Provincial Grazing Reserve (*Rocky*) in central Alberta, Canada..... 18

Figure 2.2b. Example of landscape configuration at the *Black Bear* Provincial Grazing Reserve (*Black Bear*) in central Alberta, Canada..... 18

Figure 2.3. Experimental design within the Black Bear region..... 21

Figure 2.4a. Schematic of the bird and beetle exclusion cages..... 22

Figure 2.4b. Schematic of bird-only exclusion cages..... 22

Figure 2.5. Schematic of bird-only exclusion cage..... 23

Figure 2.6. The average proportion of pupae taken by generalist predators in each of the exclusion treatment combinations and control trees during 2003 and 2004..... 30

Figure 2.7. The residual mortality of FTC pupae as a function of density of naturally occurring pupae in 2003..... 31

Figure 2.8. The residual mortality of FTC pupae as a function of density of naturally occurring pupae in 2004..... 32

Figure 2.9. Residual predation of FTC pupae in continuous and isolated stands of aspen forest..... 33

Figure 2.10. The linear effect of pupal density on predation rates by generalist predators on reference trees in 2003 and 2004..... 34

Figure 2.11. Residual pupal mortality in forest fragments at varying distances to the nearest continuous forest tract in 2003 and 2004..... 35

Figure 2.12. Parasitism of remaining pupae in each of the exclusion treatment combinations and control trees after predation was allowed to occur in 2003 and 2004..... 37

Figure 2.13. Residual parasitism of forest tent caterpillar pupae after predation in 2003..... 38

Figure 2.14. Residual rate of parasitism of forest tent caterpillar pupae after predation in 2004..... 38

Figure 3.1. Example of bird type predation characterized by a 'clean' tear in the cocoon and the complete removal of the pupa..... 60

Figure 3.2. Example of beetle type predation characterized by the presence of the pupal casing and the shredded cocoon..... 60

Figure 3.3 The average proportion of pupae scored as bird or beetle type predation in 2003 and 2004..... 65

Figure 3.4. The average proportion of pupae scored as *bird-type* predation on trees from which beetles were excluded in continuous forest tracts and isolated forest fragments, in 2003 and 2004..... 67

Figure 3.5. The average proportion of pupae scored as *beetle-type* predation on trees from which birds were excluded in continuous forest tracts and isolated forest fragments in 2003 and 2004..... 68

Figure 3.6. The residual mortality of forest tent caterpillar pupae depredated by birds, as a function of pupal density in 2003 and 2004..... 68

Figure 3.7. The residual mortality of forest tent caterpillar pupae depredated by beetles, as a function of pupal density in 2003 and 2004..... 68

Figure. 3.8. Residual beetle predation as a function of patch size fit with a non-linear spline smoother after controlling for year, structure, and prey..... 71

Figure. 3.9. Residual beetle predation as a function of patch isolation distance from the nearest tract of continuous forest, fit with a spline smoother after controlling for year, forest structure and prey density..... 71

Figure 3.10. Residual predation rates of FTC pupae exhibited by beetle predators with increasing vegetation cover, after controlling for year, forest structure and prey density..... 73

Figure 3.11. The abundance of avian predators of forest tent caterpillars in 2003 and 2004, in the Black Bear and Rocky regions..... 74

Figure 3.12. The average number of avian predators in continuous forest tracts and isolated forest stands in 2003 and 2004..... 74

Figure 3.13. The residual mortality of FTC pupae with increasing beetle abundance including *P. melanarius*..... 76

Figure 3.14. The residual mortality of FTC pupae with increasing beetle abundance, excluding *P. melanarius*..... 76

Chapter 1

General Introduction

INTRODUCTION

The forest tent caterpillar (FTC) *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) is an economically important pest of North American deciduous forests and is found throughout most of the United States and Canada. FTC are highly polyphagous across their range, and consume foliage from a variety of trees including sugar maples (*Acer saccharum* Marsh.), water tupelo (*Nyssa aquatica* L.), swamp black gum (*Nyssa sylvatica* L.) (Batzer and Morris 1978), and a number of fruit trees (Lowe 1899; Weed 1899). In western Canada, specifically Alberta however, oviposition and early instar feeding occurs on trembling aspen (*Populus tremuloides* Michx). More mature larvae will also consume foliage from balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.) and alder (*Alder* sp.).

Life History

As with other species of tent caterpillars, FTC are univoltine, with all active stages present during the spring and summer months. In July and early August, fertilized female moths oviposit bands of 60 to 400 eggs on host trees (Parry 1994). With each individual egg laid, the female moth releases a white substance called spumaline. This covering dries and hardens and is thought to protect against natural enemies and inclement temperatures (Hodson 1941). Within the egg band, embryos quickly develop into first instar larvae that remain encased within each egg capsule over the winter months (Hodson 1941; Weed 1899, 1900). In the spring, increasing ambient temperatures appear to induce hatching of the first instar larvae, which is generally synchronized with the bud burst of host trees (Hodson 1941). Early instar larvae of the FTC are highly gregarious and feed in family colonies, moving from resource to rest sites using pheromones and silk threads (Colasurdo and Despland 2005). During the fourth and fifth instars however, caterpillars enter a solitary phase and begin to disperse to neighbouring trees to feed and rest (Parry 1994).

Beginning in early July and extending into August, fifth instar larvae begin to pupate. Typically, larvae fold together one or more leaves, knitting them with silk. Upon completion of the outer cocoon, they begin to spin an inner cocoon that is characterized

by a tightly spun, relatively thick silk layer. At high densities, defoliation may be so extensive that larvae will spin cocoon on branches without leaves, among evergreen needles, along bark crevices, or in the grass. Within the cocoon, the sedentary pupa undergoes compete metamorphosis in 10 to 14 days after which it emerges as an adult moth.

Generalist predators of tent caterpillars.

Late larval stages of the forest tent caterpillar have well pronounced setae that act as a deterrent to predators. Many birds and predaceous ground beetles are nonetheless able to feed on both the larvae and pupae of FTC. In particular, the Baltimore oriole (*Icterus galbula* Linnaeus) is a very important predator. These birds rip open the cocoons and pull out the pupae from within (Parry 1994; Sealy 1980). Parry (1994) reported that orioles were the most important pupal predator in some areas in Alberta, often causing more than 90% mortality. Similarly, Weed (1899) observed small birds such as nuthatches and chickadees tearing open cocoons and feeding on the pupae. Thus it appears that avian predators are not restricted to any particular size class. The carabid beetle *Calosoma frigidum* (Kirby) is also known to being an important predator of FTC, particularly in the canopy as these beetles frequently climb trees in search of prey (Larochelle 1990). Other beetle predators of FTC include *Calosoma calidum* (Fabricius), *C. monoliatum* (LeConte) and, *Carabus taedatus* (Fabricius) (Larochelle 1990; Witter and Kulman 1972).

Population dynamics of forest tent caterpillars

Every 10 to 12 years, populations of FTC experience dramatic numerical increases which can last up to five years (Hodson 1941). In outbreak years there may be as many as 4 million larvae per hectare, resulting in widespread defoliation of forests (Canadian Forest Service 1991). Repeated defoliation of trees commonly results in a noticeable reduction in radial trunk growth (Hogg *et al.* 2002) and occasionally in tree death. This in turn results in economic losses for the timber industry in Canada (Hildahl and Reeks 1960). Following years of outbreak, however, population levels decrease and generally remain low for many generations. Because such population fluctuations occur throughout their

geographic range (Witter and Kulman 1972), there is much interest in trying to understand the factors determining FTC population cycles.

Most studies have focused on the factors involved in the decline phase of FTC population cycles. Populations of numerous specialist parasitoid species are tightly coupled to those of the forest tent caterpillar (Clark 1958; Hodson 1941; Parry 1995; Witter and Kulman 1972; Witter and Kulman 1979). Tight coupling of host-parasitoid interactions is thought to be a major factor associated with population declines. Similarly, the rate infection by a nuclear polyhedrosis virus increases during outbreaks and has been implicated as a factor causing the rapid decline of FTC densities. Furthermore, factors such as inclement weather (Roland *et al.* 1998), genetic factors (Ginzburg and Taneyhill 1994; Rossiter 1994) and starvation may also influence the duration and decline of population outbreaks.

Generalist predation

Rarely have the factors responsible for maintaining endemic populations of FTC been investigated. Generalist predators however, may be able to regulate insect populations around a low density equilibrium (Parry 1994; Liebhold *et al.* 2000; Southwood and Comins 1976). Predators of other forest insects are important mortality agents at low densities (Campbell 1975; Floyd 1996) however, there are conflicting data supporting (Raymond *et al.* 2004; Roland 1994) and refuting (Elkinton *et al* 2004; Liebhold *et al.* 2000) the notion of such regulation. The synoptic model proposed by Southwood and Comins (1976) suggests that cyclic forest insects have two stable equilibria, one of which is found far below the carrying capacity of the environment. Insect populations are theoretically maintained at this low population level by a combination of functional and numerical responses by predators. Because generalist predators rely on many prey resources whose abundance in the environment differ independently from one another, they are limited in their numerical responses to increased pest populations. Predators exhibiting a sigmoid or type III functional response to increasing prey densities however, are theoretically capable of such regulation (Holling 1965). Such a response is a function of the predators' search efficiency and handling time of the prey (Holling 1965). As prey numbers decrease, predation pressure subsides, preventing local extinction at very

low density. Alternatively, as prey populations increase, predators accelerate their feeding rates in response to increasing abundance of prey. At densities where predator satiation occurs, prey can escape to the upper equilibrium and an outbreak ensues. Variation in predator numbers, feeding rate and spatial heterogeneity can alter the density at which prey escape to this upper, high density equilibrium (Southwood and Comins 1976). Parry (1994) hypothesized that FTC populations do in fact have both a low density equilibrium and a less stable high density equilibrium, and suggested that generalist predators are responsible for maintaining low densities. He further suggested that small environmental perturbations in forest types that support few natural enemies may cause the release of FTC populations to the less stable outbreak equilibrium, creating spatially isolated hotspots from which outbreaks could spread.

Forest fragmentation

Roland (1993) suggested that increased amount of edge habitat associated with forest fragmentation decouples the host-parasitoid interactions that are thought to be important in the collapse of FTC outbreaks. It is unknown however, whether forest fragmentation has a similar effect on predator-prey interactions. Agriculture, oil and gas production and timber harvesting are three major industries in Alberta, and causes large-scale forest fragmentation, which in turn has been implicated in bird and beetle community changes. For example, bird communities have been shown to differ between fragmented and contiguous landscapes (Hobson and Bayne 2000; Norton and Hannon 1997); species richness tends to increase in fragmented landscapes (Hobson and Bayne 2000) but often there is a reduction in the abundance of long distance migrants and interior forest species (Hobson and Bayne 2000; Norton and Hannon 1997). Such changes may result from factors such as increased nest predation and parasitism along habitat edges (Andren 1995; Paton 1995). Similarly, fragmentation can negatively affect carabid beetle populations (Pearce *et al.* 2003), due in part to the invasion by habitat generalists from the surrounding matrix, leading to increased interspecific interactions and decreased abundance of forest dwelling species (Burke and Goulet 1998). Forest fragmentation therefore, may have a negative effect on FTC predator abundance by hindering predator-prey interactions.

Thesis overview

Little is known about the impact that generalist predators have on FTC populations. The main objectives of this thesis are: 1) to assess the magnitude of generalist predation on FTC, across a range of FTC densities, and 2) to determine whether generalist predation is decreased in forest fragments. I examine the combined and separate effects of bird and beetle predators on populations of FTC by assessing rates of predation recorded from exclusion treatments. I used a crossed design that either allowed or did not allow birds and/or beetles from accessing deployed FTC pupae on experimental trees. The four treatments were therefore; 1) both beetles and birds excluded, 2) just birds excluded, 3) just beetles excluded, and 4) no predators excluded. Furthermore, the effects of fragmentation are assessed by establishing these four treatments in both a continuous tract of forest and forest fragment, with which it was paired.

In Chapter 2, I assess the interactive effects of predator types (birds and beetles) to determine whether they inflict additive or compensatory predation. For this, I assume 1) that the majority of predation in cages from which birds were excluded, was caused mainly by beetles, 2) that predation in cages from which beetles were excluded, was caused mainly by birds, and 3) that predation on trees in which no predators were excluded was caused by mainly birds *and* beetles. It is acknowledged however, that a portion of predation recorded from these experimental trees was likely caused by other mortality agents such as ants, pentatomids and potentially arboreal vertebrates (Witter and Kulman 1972). Although other predators may have been present, this analysis will lend insight into how some predator guilds impact the predation rates of other predators.

In Chapter 2, I also estimate the pattern of predation by all generalist predators along a gradient of FTC densities to determine whether there is evidence of regulation of low density FTC populations. Furthermore, the effect of fragmentation on generalist predation is assessed by comparing predation rates in forest fragments versus continuous forest tracts. In addition, the effect of landscape configuration is assessed by examining the effects of fragment size, connectedness and isolation distance on predation by all generalist predators. The effects of pupal parasitism on predation rates will also be

addressed as parasitized prey can alter predation responses of predators (Jones *et al.* 2005; Roland 1990).

In Chapter 3, I ask similar questions to those posed in Chapter 2; however, I do so based explicitly on predation rates exhibited by birds only and by beetles only, on deployed pupae. These data were obtained from cages from which beetles or birds were excluded respectively, and only predation that was characteristically bird or beetle was used for the analysis. By doing so, I am able to evaluate the individual patterns of predation by birds and beetles to changes in FTC densities. I also evaluate the guild-specific effects of habitat fragmentation on bird-inflicted and beetle-inflicted predation rates. I also address whether bird predators show any evidence of a numerical increase at high FTC densities, and in doing so, also assess whether predator abundance within each guild has any effect on the guild-specific predation rates.

In Chapter 4, I present a summary and short discussion of the results obtained in Chapters two and three. Furthermore, I discuss some possible avenues of future research that I believe would be useful in the understanding of FTC population dynamics.

LITERATURE CITED

Andren H. 1995. Effects of landscape composition on predation rates at habitat edges. pages. 225-255 *in* L. Hansson, L. Fahrig, G. Merriam, editors. Mosaic Landscapes and Ecological Processes, Chapman & Hall, London.

Batzer, H. O. and R. C. Morris. 1978. Forest Tent Caterpillar. USDA *Forest Service, Northeastern Region, Forest Insect & Disease Leaflet* **9.**

Burke, D. and H. Goulet. 1998. Landscape and area effects on beetle assemblages in Ontario. *Ecography* **21**:472-479.

Campbell, R. W. 1975. The gypsy moth and its natural enemies. USDA *Agricultural Information Bulletin* **381**.

Canadian Forest Service. 2001. Forest tent caterpillar. *Frontline Express, Great Lakes Forestry Centre Bulletin* **9**:1-2.

Clark, E. C. 1958. Ecology of the polyhedroses of tent caterpillars. *Ecology* **39**:132-139.

Colasurdo, N. and E. Despland. 2005. Social cues and following behavior in the forest tent caterpillar. *Journal of Insect Behavior* **18**:77-87.

Elkinton, J. S., A. M. Liebhold, and R. M. Muzika. 2004. Effects of alternative prey on predation by small mammals on gypsy moth pupae. *Population Ecology* **46**:171-178.

Floyd, T. 1996. Top-down impacts on creosote bush herbivores in a spatially and temporally complex environment. *Ecology* **77**:1544-1555.

Ginzburg, L. R. and D. E. Taneyhill. 1994. Population-cycles of forest Lepidoptera - a maternal effect hypothesis. *Journal of Animal Ecology* **63**:79-92.

Hildahl, V. W. A. Reeks. 1960. Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hübner, and their effects on stands of trembling aspen in Manitoba and Saskatchewan. *Canadian Entomologist* **92**:199-209.

Hobson, K. A. and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixed woods of western Canada. *Wilson Bulletin* **112**:373-387.

Hodson, A. C. 1941. An ecological study of the forest tent caterpillar, *Malacosoma disstria* Hbn. USDA *Minnesota Agricultural Experiment Station Technical Bulletin* **148**

Hogg, E. H., M. Hart, and V. J. Lieffers. 2002. White tree rings formed in trembling aspen saplings following experimental defoliation. *Canadian Journal of Forest Research* **32**:1929-1934.

Holling, C. S. 1965. The functional response of predators to prey density. *Memoirs of the Entomological Society of Canada* **45**:1-60.

Jones, G. A., K. E. Sieving, M. L. Avery, and R. L. Meagher. 2005. Parasitized and non-parasitized prey selectivity by an insectivorous bird. *Crop Protection* **24**:185-189.

Larochelle, A. 1990. The Food of Carabid Beetles (Coleoptera: Carabidae, Including Cicindelinae). Faberies Supplément 51-132.

Liebhold, A., J. Elkinton, D. Williams, and R. M. Muzika. 2000. What causes outbreaks of the gypsy moth in North America? *Population Ecology* **42**:257-266.

Lowe, V. H. 1899. The forest tent caterpillar. USDA *New York Agricultural Experiment Station Bulletin* **159**.

Norton, M. R. and S. J. Hannon, 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Canadian Journal of Forest Research*. **27**:44-53.

Parry, D. 1995. Larval and pupal parasitism of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) in Alberta, Canada. *Canadian Entomologist* **127**:877-893.

Parry, D. 1994. The impact of predators and parasitoids on natural and experimentally created populations of forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). Masters Thesis, University of Alberta, Alberta.

Paton, P. W. C. 1994. The effect of edge on avian nest success - how strong is the evidence. *Conservation Biology* **8**:17-26.

Pearce, J. L., L. A. Venier, J. Mckee, J. Pedlar, and D. Mckenney. 2003. Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. *Canadian Entomologist* **135**:337-357.

Raymond, B., A. Vanbergen, A. Watt, S. E. Hartley, J. S. Cory, and R. S. Hails. 2002. Escape from pupal predation as a potential cause of outbreaks of the winter moth, *Operophtera Brumata*. *Oikos* **98**:219-228.

Roland J. 1990. Interaction of parasitism and predation in the decline of winter moth in Canada. Pages 289-302.*in* A.D. Watt, S.R. Leather, M.D. Hunter and N.A.C. Kidd, editors. Population Dynamics of Forest Insects. Intercept Publishers, Andover.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* **93**:25-30.

Roland, J. 1994. After the decline - what maintains low winter moth density after successful biological control? *Journal of Animal Ecology* **63**:392-398.

Roland, J., B. G. Mackey, and B. Cooke. 1998. Effects of climate and forest structure on duration of forest tent caterpillar outbreaks across central Ontario, Canada. *Canadian Entomologist* **130**:703-714.

Rossiter, M. 1994. Maternal effects hypothesis of herbivore outbreak. *Bioscience* **44**:752-763.

Sealy, S. G. 1980. Reproductive responses of northern orioles to a changing food-supply. *Canadian Journal of Zoology* **58**:221-227.
Southwood, T. R. E. and H. N. Comins. 1976. Synoptic population model. *Journal of Animal Ecology* **45**:949-965.

Weed C., M. 1899. The forest tent caterpillar. *New Hampshire College Agricultural experiment Station Bulletin* **64**:75-98.

Weed, C. M. 1900. The forest tent caterpillar. *New Hampshire College Agricultural Experiment Station Bulletin* **75**:107-132.

Witter, J. A., and H. M. Kulman. 1972. A review of the parasites and predators of tent caterpillars (*Malacosoma* spp.) in North America. *Minnesota Agriculture Experimental Station Technical Bulletin* **289**.

Witter, J. A. and H. M. Kulman. 1979. Parasite complex of the forest tent caterpillar (Lepidoptera, Lasiocampidae) in northern Minnesota. *Environmental Entomology* **8**:723-731.

Chapter 2

The effects of forest fragmentation on generalist predation of forest tent caterpillars (*Malacosoma disstria* Hübner) in Alberta, Canada.

INTRODUCTION

The forest tent caterpillar (FTC) *Malacosoma disstria* (Hübner), a univoltine species of Lepidoptera, is an important cyclical defoliator of North American deciduous forests. Population eruptions occur in Canada on average, every 10 to 12 years (Hildahl and Reeks 1960; Sippell 1962) during which there may be up to 4 million individual larvae per hectare (Canadian Forest Service 1991), causing complete defoliation of forest stands (Witter 1979). During these periods of extensive defoliation FTC is often implicated as a source of economic loss for the pulp and paper industry (Hildahl and Reeks 1960). Following three to eight years of consecutive outbreaks (Witter 1979), FTC population densities decrease to innocuous levels and remain so for several generations (Hodson 1977).

Of great interest to both empirical and theoretical ecologists is the identification of the factors and mechanisms responsible for the outbreak and suppression of cyclic insect populations. Suggested factors include changes in host plant quality (Larsson *et al.* 2000), weather (Roland *et al.* 1998), maternal effects (Ginzburg and Taneyhill 1994; Rossiter 1994), pathogens (Parry 1995), parasitoids (Parry *et al.* 1997; Roland and Taylor 1997; Stark and Harper 1982) and generalist predators (Elkinton *et al.* 2004; Parry 1994; Weseloh 1988). Much of the literature on FTC focuses on agents responsible for the suppression of outbreaks. Parasitoids and a nuclear polyhedrosis virus (NPV) appear to be important mortality factors at high density and declining phases of FTC population cycles (Clark 1958; Sippell 1962; Witter 1979; Witter and Kulman 1972) but factors maintaining low density populations and mechanisms initiating outbreaks are not well understood. There is however, extensive literature on the mortality agents during the endemic phase of other cyclic forest insects. For example, gypsy moth studies have revealed that generalist predators can inflict high predation pressure (Gould *et al.* 1990) and may be able to regulate low density populations (Campbell 1975). Known generalist predators of FTC include several species of birds, amphibians, predaceous ground beetles and spiders (Weed 1899; Witter and Kulman 1972). High rates of bird predation have been recorded in small, localized areas during years of outbreak and in response to artificially augmented populations of FTC (Hodson 1941; Parry *et al.*1997; Sealy 1980).

Similarly, beetle predation has been studied only during years of FTC outbreaks. The combined impact that these two guilds of predators have on FTC populations has not been quantified to date, nor has their effect been assessed across a range of naturally occurring FTC densities. A goal of this chapter is to assess the potential functional responses of generalist predators and their cumulative effect on FTC populations.

Generalist predators depend on FTC as a food resource during only part of the year, resulting in a limited ability to respond numerically to increasing prey density (Hanski 1990). Predators therefore, are thought to respond to increasing prey densities through both numerical and functional responses (Oaten and Murdoch 1975). The sigmoid, or type III functional response occurs in predators that increase their search activity with increasing prey density. It is the only functional response that is considered regulatory because the number of prey consumed by an individual predator increases with prey density. Polyphagous predators are thought to exhibit such responses due to their ability to switch to the more abundant prey resource. The combined effect of the numerical and functional response of predators can be assessed by determining the predation rate (the proportion of prey consumed by predators) or the predation risk of the prey, over a range of prey densities (Case 2000). If predators are responsible for maintaining or regulating sparse FTC populations, their actions must be mediated through a pattern of positively density-dependent predation rates over at least part of the range of host density (Holling 1965). As such, at very low densities predation risk of the prey is minimal and predators take a small proportion of the prey. As the prey population grows however, predators consume proportionally more prey until they reach the point of satiation (Oaten and Murdoch 1975; Schauber *et al.* 2004). This threshold prey density is the point at which prey 'escape' from predators and outbreaks can occur, resulting in decreased predation rates. Alternatively, predation rates (or 'risk' to the prey) maybe high at low densities, but decreases as prey density increases, resulting in an inversely density-dependent relationship (Holling 1965). This pattern of predation is indicative of predators randomly encountering prey and can be described by the type II functional response (Holling 1965). It is considered destabilizing because the per capita rate of predation is maximal at the lowest prey density, and can lead to local extinction of prey

(Southwood and Comins 1976). There has been considerable debate in the literature as to the shape that generalist predation takes in forest insect systems. Some studies have argued that predation of gypsy moth pupae follows a regulating pattern (Campbell 1975) but others have contested this and found inversely density-dependent predation (Elkinton *et al.* 2004). The literature on winter moth appears to be more consistent in finding positive density-dependent predation rates, particularly for pupae (Raymond *et al.* 2002; Roland 1994). Various factors, including habitat fragmentation and differences in habitat quality may modify the shape of the functional responses exhibited by predators (Elkinton *et al.*2004; Raymond *et al.* 2002; Roland 1993). Predation may also be modified by the presence of parasitized prey. Both Roland (1990) and Jones *et al.* (2005) found that some predators preferentially consumed unparasitized prey. Birds and beetles therefore, may respond to the presence of parasitized prey and could modify the impact of their predation on FTC.

The effects of habitat fragmentation on biodiversity have been well documented in the literature, but increasingly studies have focused on how species interactions are modified by landscape heterogeneity (Hanski 1994; Roland 1993). Roland (1993) found that FTC outbreaks were prolonged in fragmented forests suggesting that there was an uncoupling of specialist parasitoids and FTC interactions. Generalist predation may also be reduced in isolated forest stands either because fragmented landscapes reduce movement of predators into isolated patches, or because fragments are of lower quality, supporting fewer predators (Hanski and Parviainen 1985). The presence of generalist predators may also differ *among* fragments depending on their size, landscape connectedness, and distance from continuous forest tracts, and thus differences in landscape configuration may alter predation rates of FTC pupae. Davis (2004) showed that the abundance of some species of forest birds was lower in smaller patches, and Halme and Niemela (1993) found that the abundance of forest-specialized carabid beetles decreased with patch size. Patch use by some organisms becomes less frequent as isolation distance increases and connectedness decreases, unless they have sufficiently high dispersal ability (Aune *et al.* 2005). I therefore, expect that predation rates in smaller, less connected or more isolated patches will be lower than in large, highly connected fragments.

In order to assess the effects of fragmentation on predation, and measure the magnitude of predation by generalist predators, predation is assessed using selective predator exclosures. I use four combinations of exclusion cages to separately prevent aerial and/or terrestrial predators from accessing experimentally deployed FTC pupae. By excluding predator types, I assess their separate and combined effects on FTC populations and thus determine whether these predator guilds act additively or in a compensatory manner. Birds and beetles are the main predators of FTC (Ramse 1972; Weed 1899, 1900; Witter and Kulman 1972) and it is assumed that most of the predation caused by aerial predators is inflicted by birds, and the predators accessing FTC prey from the ground, are beetles, thus aerial and terrestrial predators will henceforth be referred to as birds and beetles respectively. The effects of prey density and habitat fragmentation on predation are also examined, in the first case, by assessing the combined response of all generalist predators to a gradation of background FTC densities, and in the second, forest structure. In addition, predation was compared among fragments varying in size, connectedness within the landscape, and distance from the nearest continuous tract of forest. I predict that predation will be lower in more isolated and less connected stands by virtue of the perceived isolation of forest fragments by the predators. Similarly, I expect that predation will be lower in smaller fragments due to decreased abundance of predators. To assess whether predation is affected by the presence of parasitized pupae, I compare the rates of parasitism of deployed pupae recovered from trees from which all predators were excluded, to the rates of parasitism of deployed pupae recovered from trees from which either birds or beetles had been excluded.

METHODS

Study areas

Exclusion cage experiments were conducted within two regions in central Alberta (Fig. 2.1) between June and August of 2003 and 2004. The first region is approximately 37 km west of Rimbey, Alberta where four sites were located on the Rocky Mountain House Provincial Grazing Reserve, and two additional sites were situated roughly 10 km south of this grazing reserve, on privately-owned and crown-owned land. These sites combined

will be referred to as the '*Rocky*' region. Six additional sites were situated within the Black Bear Provincial Grazing Reserve region ('*Black Bear*') located approximately 45 km west of Athabasca, Alberta.

Forest tent caterpillar population densities were very different between the two regions. The *Rocky* region has been experiencing outbreak levels of FTC since 2000 (Brackenreed 2000). During the 2004 field season however, densities were declining, in part due to extremely cold winter temperatures and high parasitism rates the previous summer (Roland *unpublished data*). The *Black Bear* region had moderately low densities of FTC in both years. The last known outbreak of FTC in this region occurred between 1986 and 1988 (Pelech and Hannon 1997).

The *Rocky* study region is found within the foothills boreal ecoregion and has a moderately undulating topography. Forest fragments in this region range from 0.67 to 13.4 hectares and the isolation distance to the nearest continuous tract of forest ranged from 105m to 390m (Fig. 2.2a). The *Black Bear* region is found within the boreal mixed-wood forest of central Alberta. Forest fragments in this region range in size from 0.9 to 4.14 ha and isolation distance to the nearest continuous forest tract ranged from 120m to 390m (Fig 2.2b). This region is only slightly rolling. Forest stands in both regions are comprised mainly of trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.) and, spruce (*Picea mariana* Mill. and *P. glauca* Moench.). Under-story is composed of rose (*Rosa acicularis* Lindl.), high-bush cranberry (*Viburnum edule* (Michx.) Raf.), snowberry (*Symphoricarpos occidentalis* Hook.), red raspberry (*Rubus idaeus* L.) and wild sarsaparilla (*Aralia nudicaulis* L.). Under-story of the *Black Bear* region also included buffalo berry (*Shepherdia canadensis* (L.) Nutt.), gooseberry (*Ribes oxyacanthoides* L.) and saskatoon (*Amelanchier alnifolia* (Nutt.) Nutt. ex. M. Roemer).

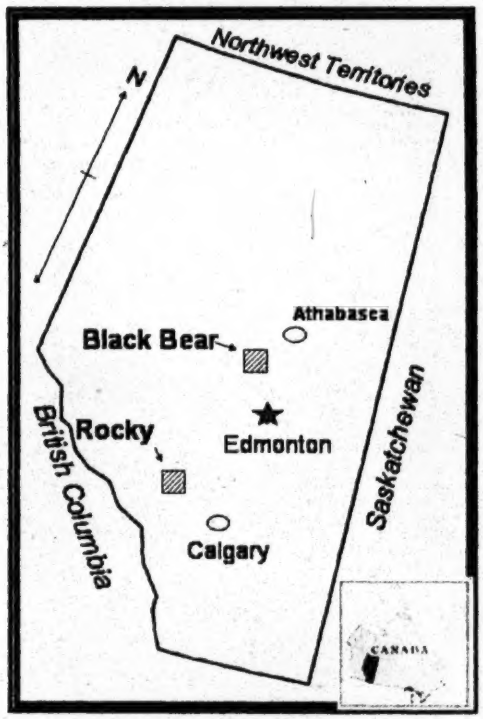

Figure 2.1. Locations of experimental regions within Alberta, Canada. The Black Bear Provincial Grazing Reserve (*'Black Bear'*) is located approximately 100 km north of Edmonton, Alberta, Canada and the Rocky Mountain House Provincial Grazing Reserve (*'Rocky'*) is located approximately 200 km southwest of Edmonton.

Approximately 60% of the landscape at both locations is pasture on which cattle graze from mid-May to mid-October. The expansion of the oil and gas industry is a large contributor to forest fragmentation and habitat loss in both regions.

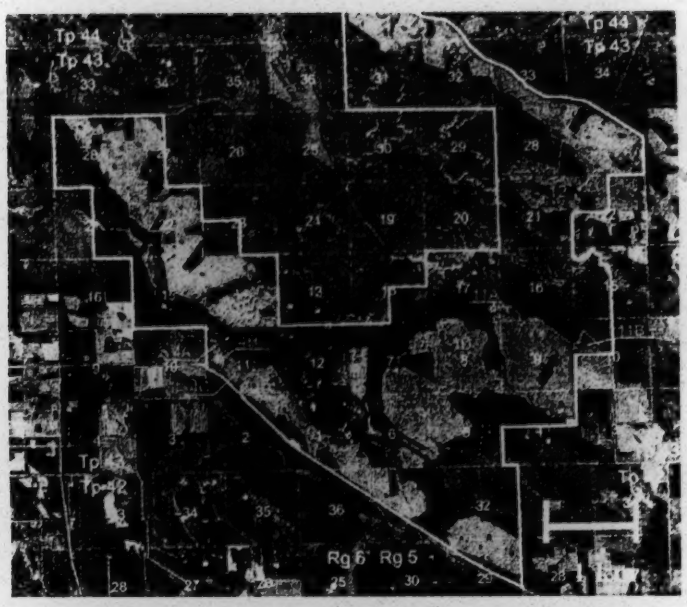

Figure 2.2a. Example of landscape configuration at the *Rocky* Mountain House Provincial Grazing Reserve (*Rocky*) in central Alberta, Canada. (*Photo source: Alberta Government, 2003)*

Figure 2.2b. Example of landscape configuration at the *Black Bear* Provincial Grazing Reserve (*Black Bear*) in central Alberta, Canada. (*Photo source: Alberta Government, 2003*)

Guilds of generalist predators

The generalist predators of the FTC larvae include spiders, ground beetles, amphibians and birds (Witter and Kulman 1972). The main pupal predators however appear to be beetles and birds. Beetles of the genus *Calosoma* are known to prey on larvae and pupae of Lepidoptera (Larochelle 1990; Lindroth 1969). The main species in central Alberta include *C. frigidum* (Kirby), *C. calidum* (Fabricius.), *C. lepidum* (LeConte), *C. luxatum* (Say) and *C. moniliatum* (LeConte). Other resident Carabids that to feed on FTC larvae or pupae include *Carabus taedatus* (Fabricius) and *Pterostichus melanarius* (Illiger) (Larochelle 1990).

There are over 60 species of birds that prey on tent caterpillars (Blomme 1991; Parry 1994; Pelech and Hannon 1995; Sealy 1979; 1980; Witter and Kulman 1972). Avian predators differ in the developmental stages of FTC on which they prey. For example, Sealy (1979) documented bay-breasted warblers (*Dendroica castanea* Wilson) feeding on early instar larvae but not pupae. Baltimore orioles (*Icterus galbula* L.) in contrast, eat both larvae and pupae. The main pupal predator in Alberta appears to be the Baltimore oriole (Parry 1994).

Experimental Design

Within each study region (*Black Bear* and *Rocky*), six sites were chosen based on the presence of aspen saplings of a size that could be readily sampled ($N_{sites} = 12$). Within each site there was an isolated forest patch paired with a section of continuous forest (Fig. 2.3). To reduce the chance of the same predators being present at more than one site, sites were separated from each other by at least 1 km. To assess the combined effects of generalist predators, and the interaction between the two predatory guilds on FTC populations, cages were used to exclude bird and/or beetle predators. Within each landscape element (fragment or continuous forest), four bendable aspen saplings of comparable size and branching patterns were selected, two of which had bird exclusion cages around them. Because predation may be biased by the presence of these exclusion cages, these trees were separated from the remaining two trees, by 50m. One of the 'bird exclusion' trees and one of the non-exclusion trees had beetles excluded from them.

There were therefore four treatments. Treatment 1 excluded both birds and beetles by using 2 cm gill netting and Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan), respectively (Fig. 2.4a). The bird exclusion cages were erected on frames of made of six 1m bamboo stakes, tied together with duct tape and secured onto the tree trunks with pipe clamps. The netting was subsequently placed over the frame and fastened to the tree trunk with twine. To prevent beetle predation, Tanglefoot was liberally applied to the entire length of the exposed tree trunk and all beetles were manually removed from the experimental tree to further reduce the likelihood of beetle predation. Treatment 2 excluded only birds and thus the cage was altered slightly so as to allow beetles free access to the interior of the cage (Fig. 2.4b). This was accomplished by attaching metal piping around the trunk of the tree, held in place with a small amount of tape and ultimately fastening the gill netting to this tubing with twine (Fig 2.5). Using this method, I ensured at least 30mm between the trunk of the tree and the metal tubing thus allowing beetles complete access to the planted pupae. Treatment 3 consisted of applying Tanglefoot to the entire length of the tree trunk to exclude only beetles and again, manually removing beetles from the tree. Treatment 4 was considered the reference on which both predator groups were present. All four treatments were applied to trees within both the fragment and continuous forest plots at each site. Furthermore, the same sites within the two regions were used in both 2003 and 2004 field seasons however, different experimental trees were selected in each year.

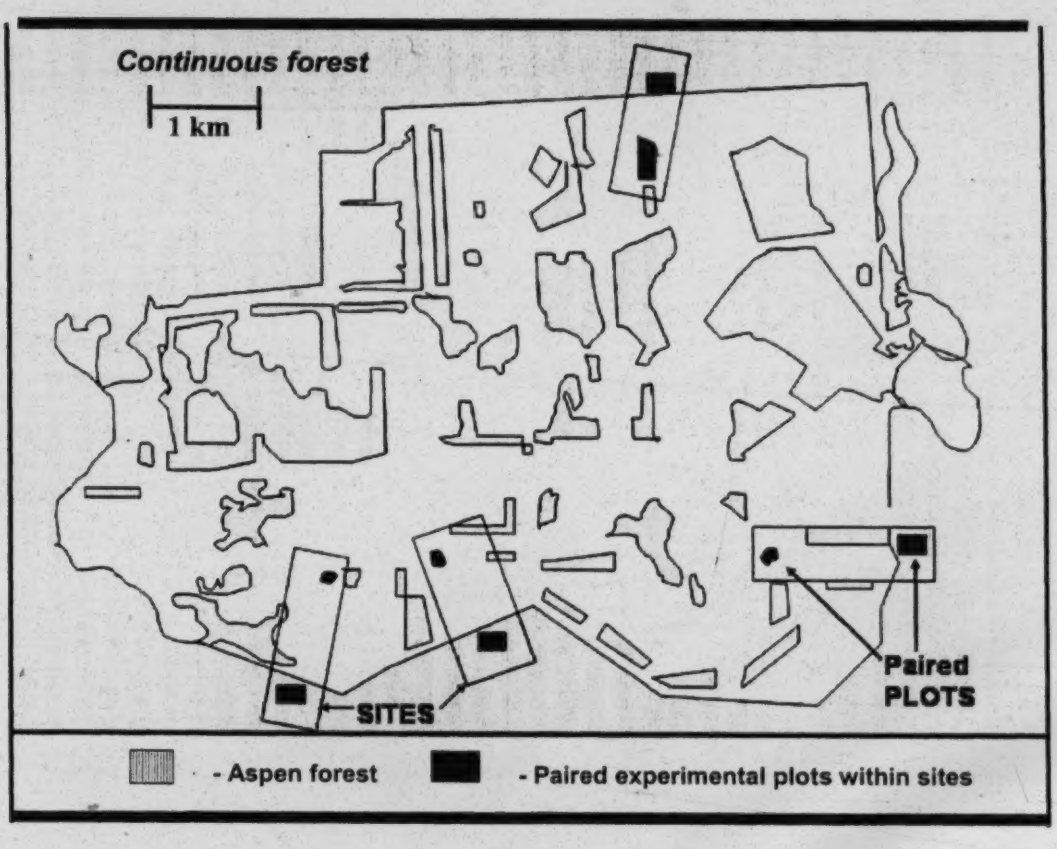

Figure 2.3. Experimental design within the Black Bear region. The design is replicated in 2003 and 2004 in 2 regions of Alberta, Canada, within in which 6 sites were chosen. Each site consisted of 2 paired plots of differing forest structure. Four exclosure treatments were located within each plot and included a crossed design of bird presence/absence with beetle presence/absence.

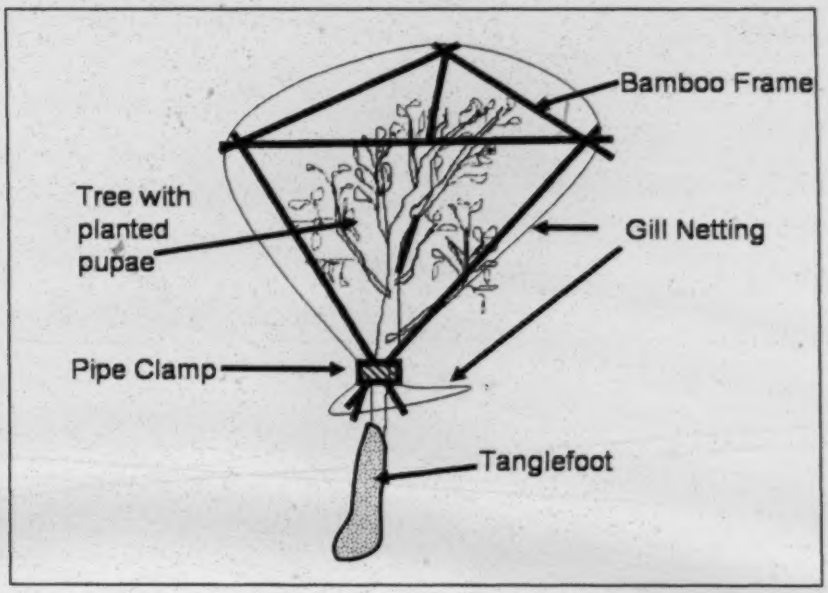

Figure 2.4a. Schematic of the bird and beetle exclusion cages.

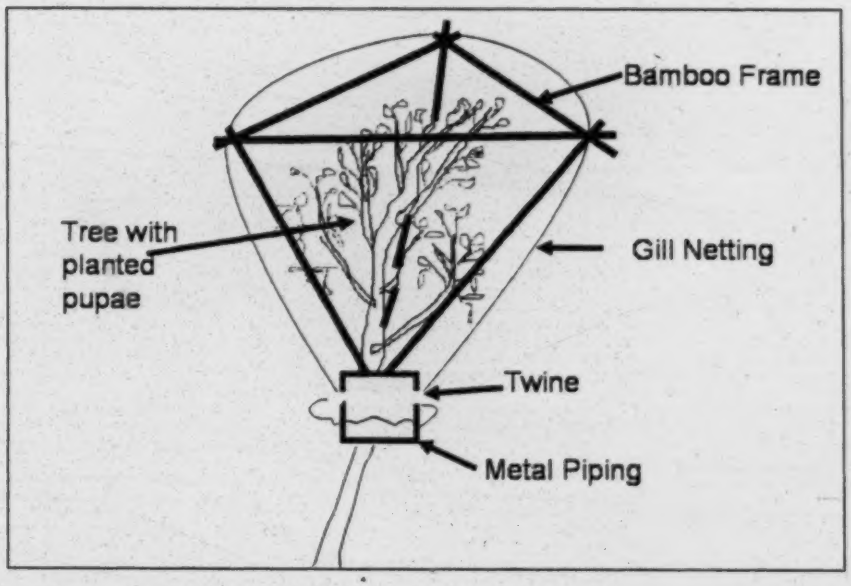

Figure 2.4b. Schematic of bird-only exclusion cages.

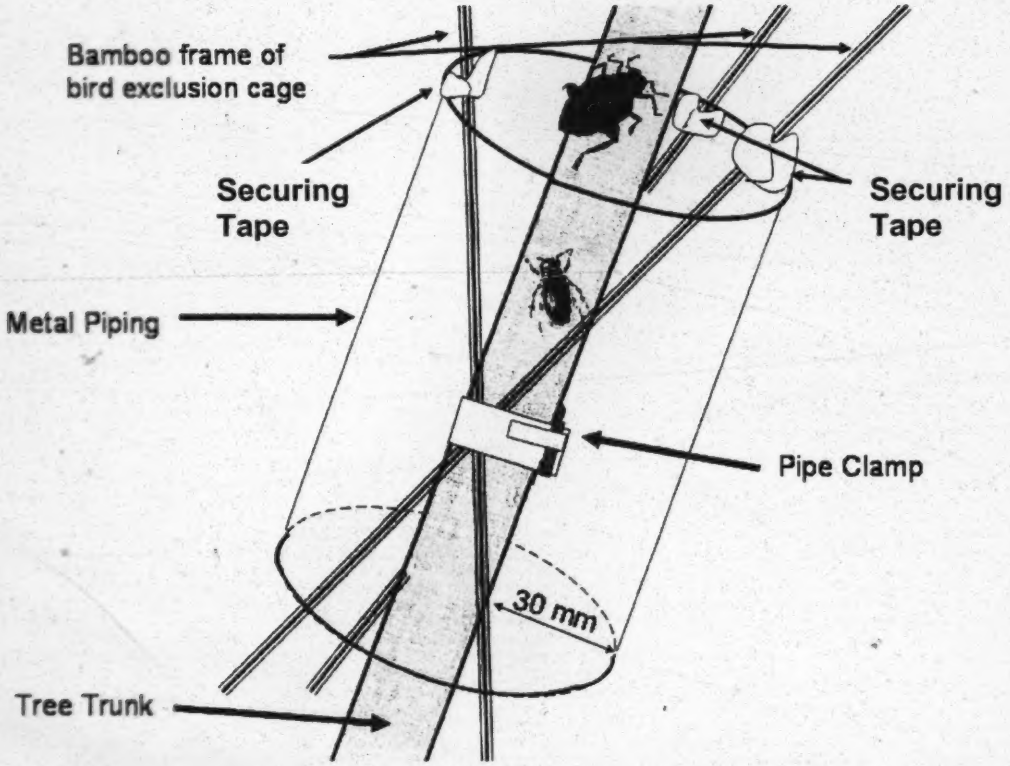

Figure 2.5. Schematic of bird-only exclusion cage, omitting gill netting fastened around the metal piping (see figure 2.4b). Metal piping was placed around individual tree trunks, allowing room for beetles to move into the canopy and access to the planted pupae. The metal piping was secured to the bamboo frame using a small amount of tape.

Estimation of pupal mortality

Three FTC pupae were deployed on each individual experimental tree ($N_{trees} = 96$). In 2003, three 5th instar larvae were placed individually in small mesh bags on each tree. Larvae were allowed to spin up in leaves prior to the bags being removed (usually within three to five days). Loss of pupae in some replicates due to factors unrelated to predation reduced this number on some trees. In 2004, pre-formed cocoons were collected in paper bags, from high density sites adjacent to the *Rocky* study region. Six cocoons were tied to each experimental tree, using twist ties, in both study regions. At high densities however, FTC will occasionally spin cocoons directly adjacent to another. Therefore, there were occasionally up to seven or eight cocoons on an experimental tree, which was

not realized until after they were returned to the lab for examination. Immediately following pupal or larval deployment, the gill netting was fastened to the bird exclusion trees. Pupae were allowed to remain on the trees for three weeks and were collected after the majority of moths had emerged in mid August. Cocoons were subsequently scored according to evidence of healthy emergence, predation or parasitism. Emergence is identified by a pupal case opened cleanly along suture lines and by the presence of moth wing scales around an emergence hole. Predation was identified by either the 'shredding' of the pupal casing and cocoon, the disappearance of pupal casing from within the cocoon or the complete disappearance of the cocoon. Pupae with characteristic parasite emergence holes or larval parasites still within the pupal case were recorded as 'parasitized'.

To estimate pupal morality within forest plots for each treatment, I calculated the proportion of planted pupae taken by generalist predators on each experimental tree:

$$\text{Pupal mortality/tree} = \frac{\#\text{ pupae preyed on by generalist predators}}{\text{Total \# pupae planted per experimental tree}}$$

Estimation of background pupal densities

To estimate background pupal densities, I conducted one 15-minute survey of cocoons in each plot, in each year. Hodson (1941) suggested that determining densities of FTC at outbreak levels may be limited by the observers' ability to collect cocoons; however; observer bias is likely similar among all high density plots. Also, at low densities, cocoons tend to be found in the canopy, often beyond the sight of surveyors. There is therefore a counting bias by observers. Without felling trees however, it would be nearly impossible to survey these cocoons. Other methods of density estimation include using pheromone traps but this method estimates density *after* pupal predation. In addition, during the dispersal phase, adult moths may enter the experimental plots from surrounding areas, obscuring local density estimates. Timed cocoon collections were therefore the most appropriate method available to estimate FTC density. Individuals conducting the survey were the same for both years to ensure consistency. A paired t-test

determined that there was no difference between observer ability ($P > 0.70$, $df = 1$, $N = 24$).

Landscape characteristics

FRAGMENT SIZE (m^2), DISTANCE (m) of the fragment to the nearest continuous patch of forest, and CONNECTEDNESS (C) of the landscape were measured using 1:30,000 scale air photos (Alberta Ministry of Sustainable Resource Development, Public Lands, 2003). Connectedness of individual fragments takes into consideration the size of the nearest patches and the distance of those patches in each of the four cardinal directions around the focal patch (Cronin 2003; Winfree *et al.* 2005):

$$C = \sum_{i} A_i e^{-Di}$$

where A_i is the area of each individual patch surrounding the fragment, D_i is the linear distance from the focal patch to the centre of the nearest patch in the ith quadrat, and e is the base of the natural logarithms. Typically this index is used to predict the colonization of a focal patch by the weighting the importance of the surrounding patches. As the surrounding patches increase in distance from the target patch, their summed weighting decreases, thus reducing the likelihood of colonization (Winfree *et al.* 2005). In the present study however, I use this index to predict the likelihood of predation by generalist predators in relation to patch connectedness as the bird and beetle predators are forest habitat specialists.

Plot characteristics

A suite of site characteristics were recorded to determine whether predation rates were related to local conditions. Increased habitat complexity may alter predator-prey interactions by increasing the number of prey refuges available to sparse prey populations and thus ensuring their local persistence, increasing prey diversity for generalist predators (Root 1973) or reducing movement and efficiency of predators (Greenslade 1964). The point-quarter method (Krebs 1989) was used to estimate total tree density and density of aspen in each patch based on four transects of 15 randomly located points in each forest plot. In addition, tree species evenness in each plot was calculated using the Simpson

index of diversity which estimates the probability that two individuals drawn at random will be different species (Simpson 1949). The probability (H') is calculated by:

$$H' = 1 - \frac{\sum [Nj(Nj-1)]}{N(N-1)}$$

where N_j is the abundance of the *j*th species and N is the total number of individuals in the sample. A value of 1 indicates perfect species evenness. This index was used to compare*/ habitat heterogeneity between plots, which may in turn affect the ability of predators to efficiently access prey (Root 1973). Within each plot, the density (m^2) of shrubs greater than 0.3 m was estimated by counting the number in four randomly located transects of 2m x 50m. A relative measure of percent coverage of herbaceous plants was visually estimated in each plot (transects were not used).

Parasitism

Predators may preferentially prey on unparasitized larvae (e.g. winter moth: Roland 1990). Parasitism was estimated in each year by determining the proportion of pupae parasitized on those trees from which all predators were excluded. I compared this to the proportion of parasitized pupae remaining after predation in the bird-only and beetle-only cages as well as those remaining on the reference trees (all predators present). If the proportion of pupae parasitized on these trees is similar to the proportion parasitized on the trees in which all predators were excluded, it suggests that predators did not selectively take unparasitized or unparasitized pupae.

ANALYSIS

Main effects: exclosure treatments, FTC density and forest structure

Data were analyzed using a mixed model in SAS (PROC MIXED, SAS Inst v.9.1. 2002). Analyses were conducted for each year separately because the experimental subjects (trees) were not used consecutively in the two years and because the method of pupal deployment differed somewhat between the two years. To control for variability in

observed predation rates that might be explained by differences in the experimental regions and paired sites, I blocked by SITEs (fragment and continuous tracts together) and nested these within the two REGIONs. These were added to the model as random factors. I did not assess the variation explained by these factors however, as their effects were not of specific interest in this study. In the following analyses, the explanatory variables BIRD EXCLOSURE, BEETLE EXCLOSURE, forest STRUCTURE and background FTC DENSITY were added to the model as fixed factors.

I first assessed predation rates in the different exclusion treatments. Of particular importance is the average predation rate occurring on trees that excluded both beetle and bird predator guilds as this gives an assessment of other mortality agents that are not affected by either treatment. The interaction between BIRD and BEETLE exclusion treatments was also assessed to determine whether predation by the two guilds of predators is either additive or compensatory.

After controlling for the effects of the exclusion treatments and of forest structure, I assessed the linear effect of background FTC density on predation rates. Finally, the effect of forest structure on total predation was examined by controlling for the effects of the exclusion treatments and background FTC density.

The proportion of planted pupae consumed by predators was arcsine square-root transformed to reduce heterogeneity of variances, in all analyses. All two-way interactions of the fixed factors were assessed but no third order interactions were examined. The Satterthwaite approximation of the degrees of freedom was used (Satterthwaite 1946).

Pattern of predation across the range of FTC densities

To identify *non-linear* effects of FTC density on predation rates over the two years, I used the predation data collected from reference trees, from which no predators were

excluded. The response variable is:

$$\textit{Proportion pupae consumed on reference trees} = \frac{\textit{number pupae preyed on by all predators}}{\textit{number pupae planted on reference tree}}$$

Initially, with only one estimate of predation per plot, I used a repeated measures analysis (PROC MIXED) to obtain residual mortality after controlling for forest STRUCTURE and YEAR, with YEAR controlling for the procedural changes in pupal deployment. SITE nested within REGION, and REGION were again added as random factors. The residual mortality from this model was then used to determine the existence of linear and non-linear effects of density (PROC GLM) over the two study years by adding quadratic and cubic density terms to the model (Elkinton *et al.* 2004)

Landscape characteristics – predation among fragments

In order to assess the effects of landscape characteristics on predation, I used data from the reference trees (no predators excluded) in the forest fragments only. I began by fitting a repeated measures Mixed Model to control for FTC DENSITY, forest STRUCTURE and YEAR, as well as SITE nested within REGION. Residual predation from this analysis was used to examine the effects of: 1) patch SIZE, 2) ISOLATION distance and 3) landscape CONNECTEDNESS on predation rates *among* fragments (PROC GLM). In addition, I explored the potential for non-linear relationships between these landscape metrics and residual predation using a Generalized Additive Model (PROC GAM) with a non-parametric spline fit of these measures to identify any non-linearity.

Plot characteristics

Using the PROC GLM, I examined the effects of aspen density, total tree density, tree diversity, percent herbaceous ground cover, and shrub layer density on residual mortality of pupae on reference trees. Residuals were obtained from the main-effects, repeated-measures model which controlled for FTC DENSITY, forest STRUCTURE, YEAR and SITE nested within REGION.

Parasitism

I used the mixed model procedure in SAS to assess parasitism rates in the presence or absence of bird and/or beetle predators. Forest STRUCTURE, background FTC DENSITY, and SITE nested with REGION were controlled for as parasitism rates are thought to be higher at outbreak densities of FTC (Hodson 1941) and may differ between forest structures (Roth 2005). Because the same experimental trees were not used in both years, I analyzed parasitism rates in each year separately. Parasitism was expressed as:

$$\textit{Proportion pupae parasitized on experimental trees} = \frac{\textit{number pupae found to be parasitized after predation}}{\textit{number planted pupae not preyed on by generalist predators}}$$

Parasitism was compared among the four exclosure treatments by adding BIRD and BEETLE exclosure treatment variables to the mixed model.

RESULTS

Main effects: exclosure treatments, FTC density and forest structure

In 2003, presence of beetles reduced survival of planted forest tent caterpillar pupae (Table 2.1). In the absence of birds, beetles consumed on average 22% of the planted pupae (Fig. 2.6). Similarly, in the absence of beetles, birds consumed 21% of the planted pupae in 2003 (Table 2.1, Fig. 2.6). The combined effects of bird and beetle predation were additive as indicated by the absence of a significant interaction (Table 2.1). Together birds and beetles removed 47% of the planted pupae from reference trees (Fig. 2.6). There was 5% mortality on trees from which both beetles and birds were excluded indicating that other sources of mortality that are not identified.

In 2004, beetles again reduced survival of planted pupae (Table 2.1) and consumed on average 25% of the pupae in the absence of birds, similar to the predation rates in 2003. Birds on the other hand did not consume a large proportion of planted pupae (Table 2.1), accounting for only 10% mortality in the absence of beetles. Predation by all predators dropped from 47% in 2003 to 27% in 2004 (Fig. 2.6) a difference attributable mainly to reduced bird predation in 2004. The interaction between predator treatments was not

significant in either year (Table 2.1) indicating that predation by birds and beetles was additive. The unexplained mortality in cages excluding both birds and beetles was only 4% in 2004, similar to the 5% in 2003.

Table 2.1. Test of fixed effects on rates of predation by generalist predators, on forest tent caterpillar pupae in, 2003 and 2004.

	2003			2004		
Parameter	**Df**	**F-value**	**P value**	**Df**	**F-value**	**P value**
STRUCTURE	1	0.00	0.71	1	0.23	0.63
BIRD EXCL	1	9.42	**0.002**	1	3.33	*0.07*
BEETLE EXCL	1	12.55	**<0.001**	1	43.12	**<0.001**
DENSITY	1	7.33	**0.008**	1	8.04	**0.006**
STRUCTURE*BIRD EXCL	1	0.00	0.95	1	0.00	0.97
STRUCTURE*BEETLE EXCL	1	1.55	0.22	1	0.57	0.45
DENSITY*BIRD EXCL	1	0.39	0.54	1	0.11	0.74
DENSITY*BEETLE EXCL	1	0.50	0.48	1	3.44	*0.07*
BIRD EXCL *BEETLE EXCL	1	0.89	0.35	1	1.35	0.25
STRUCTURE*DENSITY	1	0.14	0.71	1	1.72	0.19
Residual	81			84		

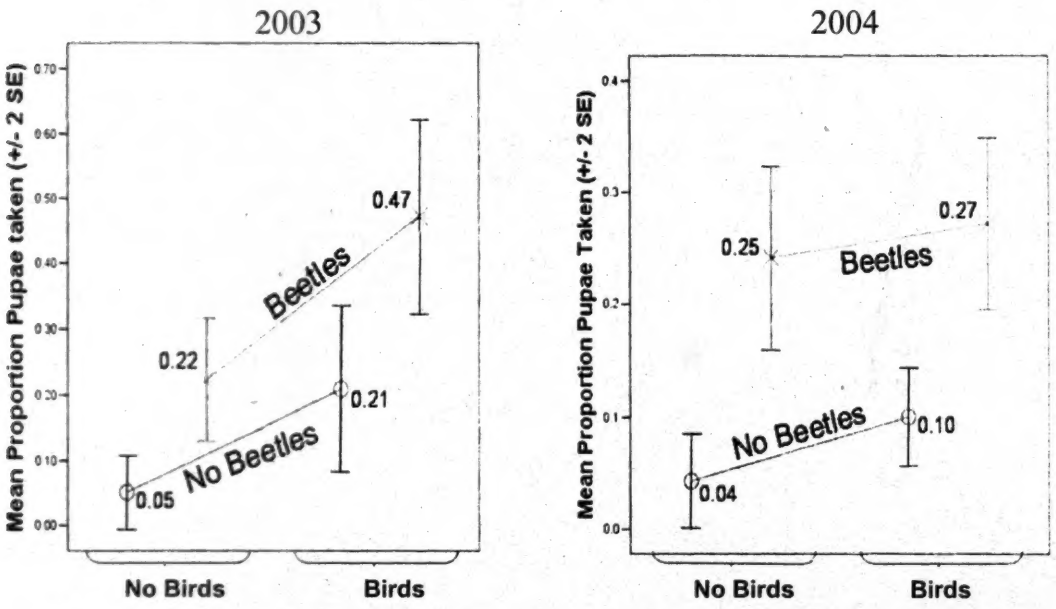

Figure 2.6. The average proportion of pupae taken by generalist predators in each of the exclusion treatment combinations and control trees during 2003 and 2004. Bars denote two standard errors of the mean.

Linear effects of FTC density

In 2003 and 2004, pupal density at *Black Bear* ranged from zero to four pupae, and zero to one per 15 minutes of searching, respectively. At *Rocky*, pupal densities ranged from zero to 404 pupae per 15 minutes and zero to 54 per 15 minutes, respectively for the two years, reflecting the phase of the population cycle in each region.

There was a significant linear relationship between proportion of pupae preyed on by generalist predators and background FTC pupal densities in both years (2003: $P < 0.01$; 2004: $P < 0.01$; Table 2.1). Pupal predation was significantly higher at low density sites than at high density sites (Fig. 2.7, Fig. 2.8). The effect of density was similar for both bird and beetle exclosure treatments (Table 2.1) in 2003 and 2004 indicating that the effect of density was similar for both predator guilds.

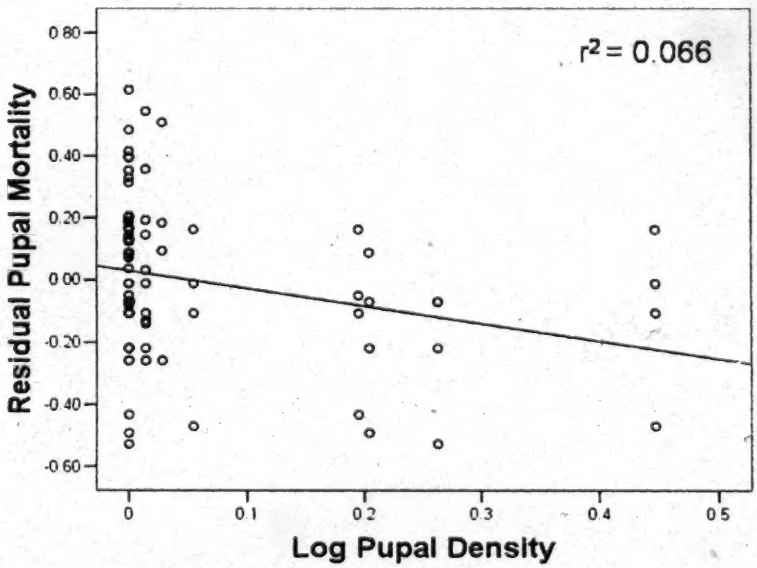

Figure 2.7. The residual mortality of FTC pupae as a function of density of naturally occurring pupae in 2003. ($r^2 = 0.066$, $P < 0.01$).

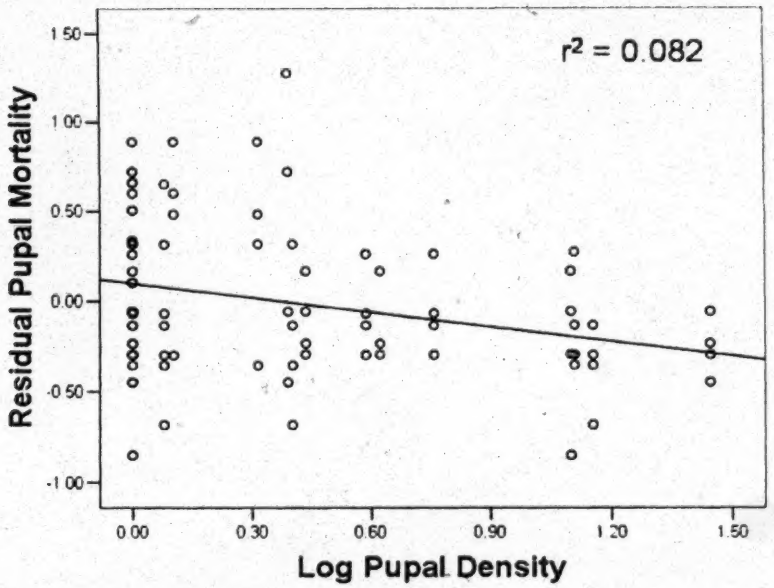

Figure 2.8. The residual mortality of FTC pupae as a function of density of naturally occurring pupae in 2004. ($r^2 = 0.082$, $P < 0.01$).

Forest Structure

There was no effect of forest fragmentation on the proportion of planted pupae consumed by predators in either year (Table 2.1, Fig. 2.9). In 2003, predation on reference trees in continuous forest tracts and isolated forest stands was 0.50 and 0.44 respectively. In 2004 predation on reference trees was identical at 0.47 in both landscape structures. There was no interaction between exclosure treatments and forest structure type on predation (Table 2.1) indicating that birds and beetles respond similarly to forest structure, at least at this scale.

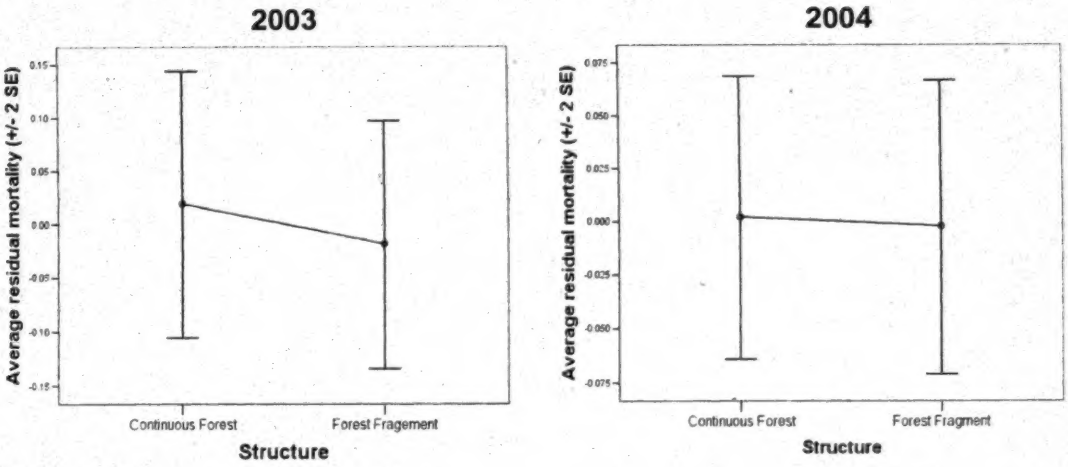

Figure 2.9. Residual predation of FTC pupae in continuous and isolated stands of aspen forest. Residual mortality is considered after controlling for FTC pupal density, exclosure treatments, site and regional differences. Bars denote two standard errors of the mean.

Pattern of predation across the range of prey densities

After controlling for the fixed effects of forest STRUCTURE and YEAR, and for the random effects of SITE and REGION, pupae on reference trees decreased linearly fashion with increasing FTC densities ($P < 0.05$, $df = 1, 37.4$. There were no non-linear effects of density on predation rate (Table 2.2). Proportionally more pupae were consumed at low densities (Fig. 2.10), indicative of a type II functional response.

Table 2.2. Parameter estimates of the non-linear fit of residual predation as a function of pupal density. Data are for reference trees, in 2003 and 2004 combined.

Parameter	Estimate	SE	Probability of > t
Quadratic model			
b_0	0.08	1.07	0.29
b_1	-0.49	-0.92	0.36
b_2	0.12	0.26	0.79
Cubic model			
b_0	0.07	0.08	0.37
b_1	-0.02	1.08	0.98
b_2	-1.04	2.37	0.66
b_3	0.62	1.24	0.62

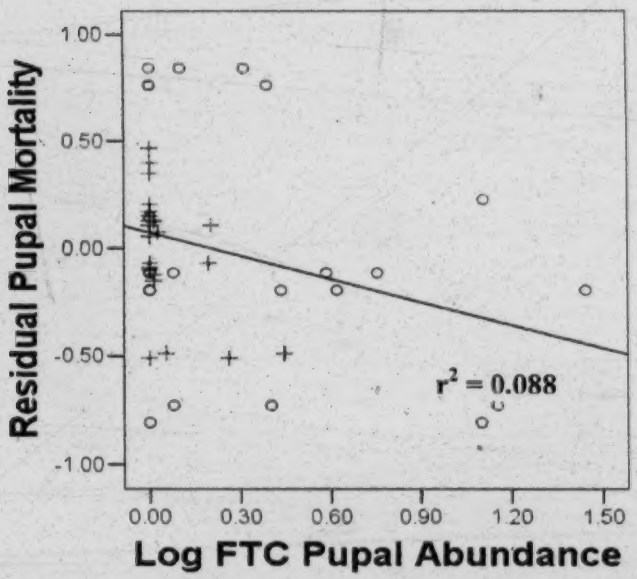

Figure 2.10. The linear effect of pupal density on predation rates by generalist predators on reference trees in (o) 2003 and (+) 2004 (r^2 = 0.088, $P < 0.05$).

Landscape characteristics – predation among fragments

Although average rates of predation did not differ between fragments and contiguous tracts of forest, predation rates may still differ among fragments varying in their characteristics and spatial configuration within the landscape relative to large tracts of forest. Residual predation from reference trees was obtained from the analysis controlling for YEAR, STRUCTURE, background FTC DENSITY and for the random effects of SITE and RESERVE. ISOLATION distance however, was significantly correlated with background FTC DENSITY in both years (2003: P = 0.037, correlation coefficient = -0.301; 2004: P < 0.029, correlation coefficient = -0.316), so I removed DENSITY from the primary analysis and used the resulting residuals to identify any effects of ISOLATION on predation.

Patch SIZE does not affect the proportion of pupae consumed by generalist predators in either year ($F = 0.01$; df = 1, 22; p = 0.92), nor is there an effect of landscape

CONNECTEDNESS (F = 0.91; df = 1, 22; P = 0.35). There is a trend of increasing predation as DISTANCE from continuous forest increases (F = 3.96; df = 1, 22; P = 0.059) (Fig. 2.11), a pattern opposite to my hypothesis. There were no significant nonlinear effects of any of the three landscape measures on predation rates (Table 2.3).

Table 2.3. Effects of forest fragment characteristics on the proportion pupae consumed by generalist predators in 2003 and 2004, combined.

Variable	Linear Effect		Non-linear Effect (Spline)	
	$F_{1,22}$	P-Value	Df	P-Value
Patch Size m^2	0.01	0.92	4	0.66
Connectedness	0.91	0.35	4	0.32
Isolation distance	3.96	**0.059**	4	0.84

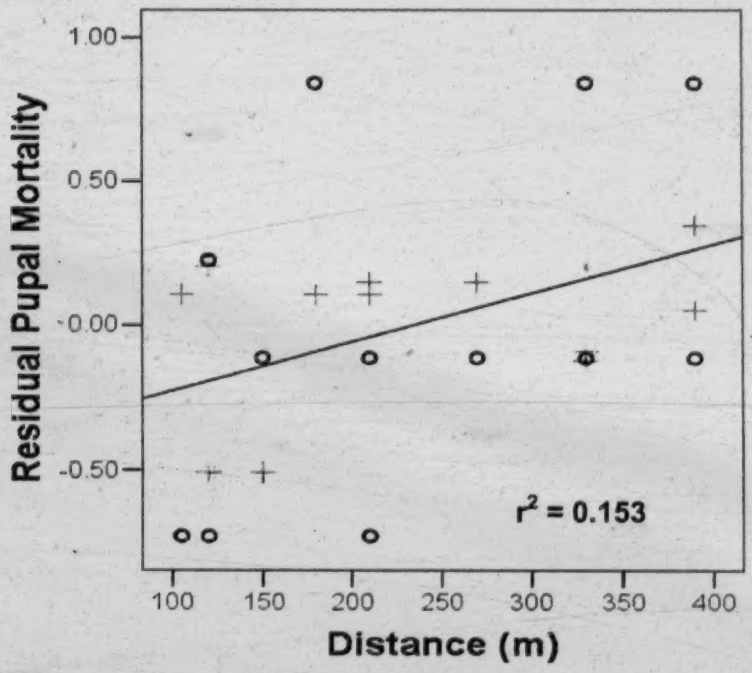

Figure 2.11. Residual pupal mortality in forest fragments at varying distances to the nearest continuous forest tract in 2003 (o) and 2004 (+) (r^2 = 0.153, P = 0.059).

Plot characteristics

The density of host trees (aspen) and the density of all trees within a patch had no effect on the residual predation (Table 2.4). Furthermore, the diversity of tree species within plots did not affect predation rates. Similarly, there was no effect of shrub vegetation density or proportion herbaceous cover on predation, a pattern which may have resulted from there being little difference in these characteristics among plots (Table 2.4)

Table 2.4. The effects of vegetation characteristics on residual mortality of forest tent caterpillar pupae.

Variable	Mean of characteristic (+/- SE)	$F_{1, 46}$	P value
Number aspen per hectare	1171 (148)	0.09	0.76
Absolute number of trees per hectare	1689 (157)	0.10	0.75
Simpson's tree diversity	0.47 (0.23)	0.001	0.95
Proportion herb cover	0.76 (0.024)	0.03	0.83
Shrub vegetation density (plants/m2)	2.34 (0.14)	0.20	0.66

Parasitism

The rates of parasitism on trees from which both birds and beetles were excluded averaged 43% in 2003 and 63% in 2004. There was no significant effect of bird presence/absence on parasitism rates in either year (2003: $F_{1, 88} = 2.79$, $P = 0.098$; 2004: $F_{1, 88} = 2.70$, $P = 0.10$; Fig. 2.12) indicating no preference by these predators for either parasitized or unparasitized pupae. There was however, a trend for high parasitism rates of remaining pupae after predation, when only birds were present (53% in 2003, 69% in 2004) suggesting that birds may preferentially cull unparasitized pupae. These trends however, were not strong. There was no effect of beetle presence/absence on parasitism rates in either year (2003: $F_{1, 88} = 1.06$, $P = 0.31$; 2004: $F_{1, 88} = 1.82$, $P = 0.18$; Fig 2.12). When both guilds were present, 60% and 65% of remaining pupae were found to be parasitized in 2003 and 2004 respectively (Fig. 2.12a & b) whereas parasitism rates of the pupae remaining at the end of the experiment were 43% and 63% in 2003 and 2004, in cages where neither guild was present. Again, this pattern indicates higher predation on unparasitized pupae.

There was no effect of forest STRUCTURE on parasitism rates following predation (2003: $F_{1, 88} = 0.08$, P = 0.78; 2004: $F_{1, 88} = 0.56$, P = 0.46) reflecting the fact that STRUCTURE did not affect predation generally. Parasitism rate of remaining pupae increased with increasing FTC density in 2003 but not in 2004 (2003: $F_{1, 88} = 7.65$, P = 0.0069; 2004: $F_{1, 88} = 1.17$, P = 0.28) (Fig 2.13 & 2.14).

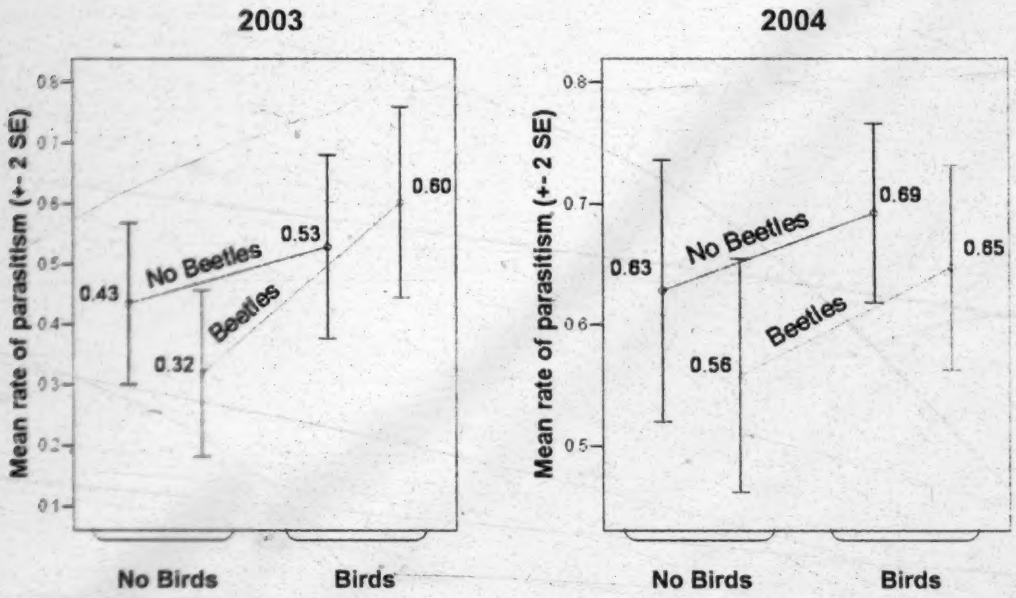

Figure 2.12 Parasitism of remaining pupae in each of the exclusion treatment combinations and control trees after predation was allowed to occur in (a) 2003 and (b) 2004. Bars denote two standard errors of the mean.

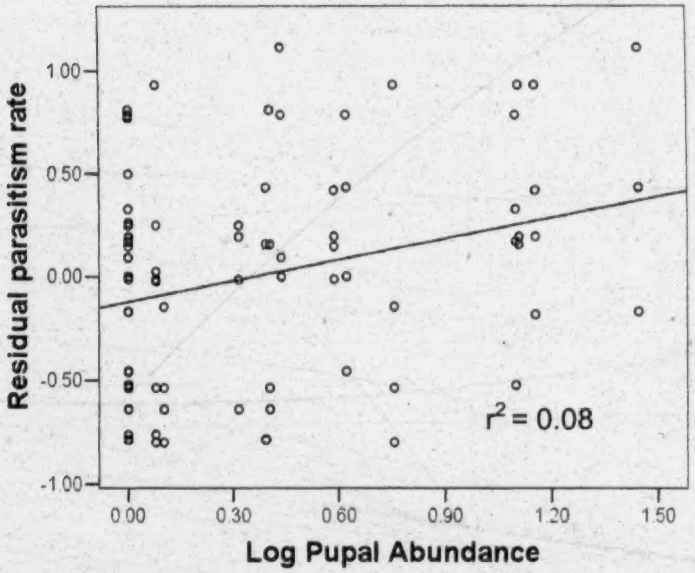

Figure 2.13. Residual parasitism of forest tent caterpillar pupae after predation in 2003 ($r^2 = 0.08$, P = 0.0069).

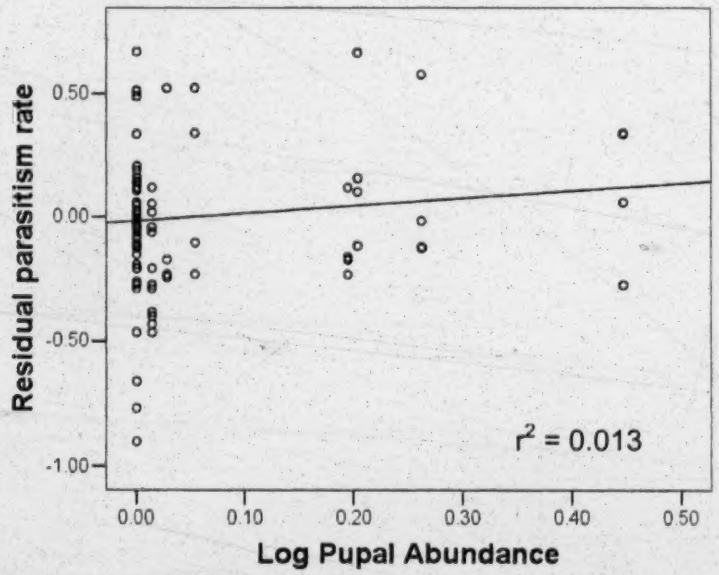

Figure 2.14. Residual rate of parasitism of forest tent caterpillar pupae after predation in 2004 ($r^2 = 0.013$, P = 0.28).

DISCUSSION

Overview

Two main goals of this chapter are:1) to assess the magnitude of predation of FTC pupae by generalist predators, and 2) to determine whether generalist predation differs between forest fragments and continuous forests. Previous studies have found that the efficacy of predators is often decreased by habitat fragmentation, presumably due to altered movement in a heterogeneous landscape (Karieva 1987). In the present study, I assumed that any effect of landscape on predation was directly due to landscape effects on predator movement. An additional goal of this chapter is to examine the shape of generalist predation across a range of FTC densities to estimate to lend insight into the factors responsible for maintaining low density populations of FTC.

Experimental Treatments

Generalist predators can inflict high or low rates of predation on insect populations (Campbell and Torgersen 1982; Crawford and Jennings 1989; Elkinton *et al.* 2004; Hanski and Parviainen 1985; Liebhold *et al.* 2005; Roland 1994). My study suggests that individually, avian and beetle predator guilds have on average a relatively low impact on FTC populations (birds: up to 21 %; beetles: up to 25% predation) compared to generalist predators of other herbivorous insects, such as the white-footed mouse that causes up to 81% of gypsy moth mortality (Liebhold *et al.* 2005). Bird and beetle predation on FTC is additive however, resulting in elevated levels of predation when both predators are present (up to 47%), indicating they both feed on pupae at the rate expected from the rate of each when they occur alone. In a similar predator exclusion experiment, Floyd (1996) found that herbivorous insect abundance on creosote bushes (*Larrea tridentata*) decreased significantly when only bird or only arthropod predators were present, and that their effect was also additive when they occurred together. Both my study and that of Floyd (1996) illustrate the importance of the combined effects of predator guilds in some predator-prey systems.

Overall predation differed between years; in 2003 generalist predators consumed 47% of the deployed pupae but in 2004, only 27% of the pupae were depredated. This difference is likely attributable to the decrease in bird-mediated predation. This differs from Floyd (1996) who found that that bird predators were consistently more important than arthropods in reducing the number of herbivorous insects over two experimental seasons. The annual differences in predation rates observed in the present study may be related to the pupal planting techniques used in the second year. In the first year, caterpillars were allowed to spin cocoons naturally on the experimental trees but in 2004, pre-spun cocoons were used and simply transplanted onto the trees. The transplanted cocoons became hardened and the leaves changed colour. Birds may be more attracted to cocoons spun in supple leaves, overlooking the dried, hardened cocoons. The abundance of FTC bird predators may also have an effect on predation rates. Elkinton *et al.* (2004) found that in years of low mouse abundance, predation of gypsy moth pupae decreased significantly. This issue however, will be addressed in greater detail in Chapter 3.

The presence of more palatable alternative prey may reduce predation rates of pest populations. For example, Elkinton *et al.* (2004) found that predation on gypsy moth pupae was greatly reduced when more palatable food resources (sunflower seeds) were available to white-footed mice, the main gypsy moth pupal predator. Alternative prey likely exists in both of my study regions and may have lead to depressed guild-specific predation rates. Alternative prey include moths and first instars larvae of the large aspen tortrix (*Choristoneura conflictana* Walker) which were abundant in Alberta over the two years of study (www3.gov.ab.ca/srd/forests/health/i_lat.html). Additional prey include the aspen two-leaf tier (*Enargia decolor* Walker), chironomids, seeds (Koenig and Knops 2001; Sealy 1979; 1980), slugs and beetle larvae (Larochelle 1990). It is not known however, whether these other food resources fluctuate widely among years, thus affecting the dynamics of FTC.

The presence of pupal parasites can decrease prey palatability and thus decrease generalist predation. For example, Jones *et al.* (2005) found that some birds feed preferentially on unparasitized larvae of the fall armyworm, *Spodoptera frugiperda*

(Smith). Similarly, small beetle larvae feed more frequently on unparasitized pupae of the winter moth, *Operophtera brumata* (L.) (Roland 1990). In the present study, the average parasitism rate of FTC pupae, in the absence of predators was lower than parasitism rates of remaining pupae in the presence of birds, suggesting that birds preferentially consume unparasitized prey. These results however, were only significant at an alpha level of 0.10 in both years but may help to explain the lower avian-mediated predation in 2004, when parasitism rates were substantially higher than in the previous year. Interestingly, Parry (1994) found that parasitized FTC pupae were occasionally opened by birds, only to be abandoned with the parasitoid maggot still within, again suggesting that birds preferentially cull unparasitized prey. In contrast, parasitism did not differ in the presence or absence of beetles, suggesting that beetles have no preference for parasitized or unparasitized prey.

Forest fragmentation

Generalist predation, assumed to be caused mainly by birds and beetles, did not differ between forest structures. These results were not expected if fragmentation reduced the abundance of predators in, or their movement to, isolated forest patches. Kareiva (1987) reported that the aggregative response of aphid predators was lower in isolated patches resulting in a delayed predation response, allowing prey to increase to outbreak levels. In the FTC system, it appears that: 1) predator movement is not impeded by the matrix between forest patches or, 2) predators are always present within or near the fragments. In the present study, the average distance between continuous forest and isolated patches was 230m. Simulations of beetle movement however, suggest that large-bodied, flightless beetles can move up to 500m within days (Baur *et al.* 2005). Furthermore, Beaudry *et al.* (1997) found the abundance of two important beetle predators of FTC pupae; *Calosoma calidum* and *C. frigidum*, remained unchanged after forest stands had been fragmented, although there was a delay in the re-establishment of *C. frigidum* populations. Because the landscapes in the provincial grazing reserves used in the current study have remained relatively constant since the early 1980s, the re-establishment of *Calosoma* beetles in fragments may not be an issue. In addition, both species of *Calosoma* beetles live for more than one year and over-winter in the soil as

adults (Lindroth 1969) resulting in relatively stable populations within forest fragments. Bird responses to fragmented forests have been well documented (e.g. Austen *et al.* 2001; Desrochers and Fortin 2000; Rail *et al.* 1997). Some forest-dwelling bird species are reluctant to travel into open spaces (e.g. Desrochers and Hannon 1997) but such responses are highly variable and are dependent on species, habitat requirements (Rail *et al.* 1997), matrix composition, weather conditions and predation risk (St. Clair *et al.* 1998). Grubb and Doherty (1999) examined home-range gap-crossings of forest birds and found that in general, movement of larger bodied species was not restricted by habitat fragmentation. In addition, area-sensitive ovenbirds (Villard 1998) are often found in isolated forest patches and frequently cross non-habitat gaps in the landscape (Bayne and Hobson 2001a; 2001b). Both studies suggest that forest birds are regularly found within forest fragments and therefore could respond to changes in FTC abundance. The effects of fragmentation on predation by birds and beetles will be examined separately in greater detail, in Chapter three.

Effect of fragment characteristics on predation

Although there were no differences in overall predation rates between continuous forest tracts and fragments, I explored the possibility that predation may differ *among* fragments exhibiting varying degrees of 1) patch connectedness 2) patch isolation distance and 3) patch size. Neither fragment size nor connectedness affected pupal predation in forest fragments. Patch size may be unimportant for some birds inhabiting isolated fragments because they have the ability to utilize a number of patches in an expanded home range or territory (Hinsley 2000). Celada (2000), for example, found that habitat patches smaller than yellow warbler (*Dendroica petechia*) territories were often occupied by warblers that simply used multiple isolated patches. He also found that even remote patches were occupied by warblers suggesting that birds can be highly vagile and use poorly connected patches. Similarly, carabids in the genus *Calosoma* are often found in open woodland habitats, characteristic of fragmented forests (Lindroth 1969) and are good dispersers (Beaudry *et al.* 1997; Crins 1980; Lindroth 1969). As a result, their abundance is likely similar among fragments of varying sizes and connectedness, leading to similar rates of predation.

Zabel and Tscharntke (1998) found that the abundance of predators of herbivorous insect in a fragmented stinging nettle habitat, decreased with increasing isolation distance. In contrast, I found the opposite pattern, with predation increasing as isolation distance increased (Fig 1.9). Hinsley (2000) modeled the cost to birds of using multiple patches in a fragmented landscape and found that energetic costs increased as distance between patches increased. Birds, and possibly beetles may forage more intensely in isolated patches before leaving (Charnov 1976), resulting in higher predation. Guild-specific predation responses to isolation, connectedness and patch size are examined more thoroughly in Chapter 3.

Pattern of predation across the range of FTC densities

Unlike specialist predators, generalists are only loosely coupled to the abundance of their prey such that there is a limited numerical response to changing prey densities (Hanski 1990; but see Morris *et al.* 1958). Nevertheless, there is evidence suggesting that generalist predators of the forest tent caterpillar can cause moderately high pupal mortality (also see: Parry 1994). Of importance however, is not just the magnitude of overall predation but also the shape of the response over a range of prey densities (Gould *et al.* 1990). Prey populations are regulated if predation is positively related to prey density over at least part of the range of densities (Takekawa *et al.* 1982). In contrast, if the proportion of prey consumed decreases monotonically with increasing density, regulation is not possible. This type of response is characterized by a lack of negative feedback on reproduction or survival and thus regulation of prey populations is not possible (Berryman *et al.* 1987; Hassell and May 1973; Turchin 1995).

In the present study, predation on FTC pupae by all generalist predators combined is inversely density-dependent across the full range of densities studied (Fig. 2.9) suggesting that generalist predators do not exert regulatory pressure on populations of forest tent caterpillars, even at low densities. It was expected that predation rates at outbreak levels would be low because generalist predators have a limited or non-existent ability to respond numerically to high prey abundance. At low densities however, predation rates were expected to be positively density-dependent over at least part of the

density range. Other studies of insects have produced inconsistent results. Campbell (1975) and Schauber *et al.* (2004) reported positive density-dependent predation on gypsy moth pupae by mice whereas Elkinton *et al.* (2004) and Gould *et al.* (1990) reported inversely density dependent predation rates on pupae of the same species. Predation rates of stable winter moth populations in England (Raymond *et al.* 2002) and in western Canada (Roland 1990) respectively, are positively correlated to background pupal densities. The results reported by Raymond *et al.* (2002) however, were not consistent in all habitats or among years, suggesting that predation rates are highly variable due to environmental conditions. Numerous arguments have been put forth explaining inversely density-dependent relationships in natural settings. These arguments, and their relationship to the current study, and to FTC generally, are discussed below.

At low densities, FTC pupae are generally found in the upper canopy, making them difficult to survey (Hodson 1941). As a result, our surveys of pupal abundance, which were restricted to the lower vegetation strata, may be biased downward, especially at low density. Therefore, estimates may lack the sensitivity required to assess density-dependent predation at innocuous population levels. Furthermore, estimates of pupal abundance at the *Rocky* sites may have been biased by the surveyors' ability to collect cocoons at a sufficiently fast pace. Hodson (1941) found that if there were more than 70 cocoons per meter squared, surveyors could no longer accurately estimate density, which likely occurred at a number of high density sites in the present study. The inability to obtain fine-grained population estimates at both high and low densities of FTC made it difficult to assess the precise slope or shape of the predation curve. On a similar note, the abundance of pupae found at individual sites in the *Black Bear* region, though lower than the *Rocky* densities, may have in fact been higher than 'innocuous levels', but our estimates again may not be sensitive enough to detect this. The fact that caterpillars and naturally occurring pupae were found in the lower canopy support this as pupae are generally found in the shrub layer, only as densities increase. Investigators have noted the difficulties in studying functional responses of predators in naturally low density pest populations (e.g. Hanski and Parviainen 1985; Hodson 1941) and have therefore deployed pupae across a range of known pest densities in areas where background

populations are naturally low, to assess the general shape of the predation curve (e.g. Elkinton *et al.* 2004; Raymond *et al.* 2002; Schauber *et al.* 2004).

The presence of alternative prey may modify the functional response exhibited by generalist predators (Elkinton *et al.* 2004; Hassell *et al.*1977; Holling 1965). In laboratory studies, Hassell *et al.* (1977) found that the functional response of some predators changed from type III to type II when prey were offered simultaneously with either more preferred or more conspicuous prey. In the presence of alternative prey, particularly large aspen tortrix, predators may begin to randomly encounter FTC pupae rather than actively seek them out, which would produce an inversely density-dependent response (Elkinton *et al.* 2004), the pattern seen for FTC in the current study. Functional responses can also be modified by the abundance of predators (Elkinton *et al.* 1996). In habitats with low predator density, prey may not be regulated at lower densities, resulting in outbreaks (Hanski and Parviainen 1985). Elkinton *et al.* (1996) hypothesized that during years of low mouse-predator abundance, caused by acorn-mast failure, gypsy moth populations would be released from regulatory control. In that particular study there was evidence that temporal fluctuation in predator abundance influenced gypsy moth dynamics. Long term studies examining both generalist predator and FTC abundances over time, would be required to determine whether similar pattern occur in the FTC system. In Chapter 3, the potential effect of predator abundance is assessed by examining the effect of abundance of the individual predator guilds on predation.

Although my study suggests that generalist predators do not regulate FTC populations, it is well documented that FTC abundance remains low for many years between outbreaks. A combination of mortality factors may be important during this phase of the FTC cycle. Parry (1994) found that a number of parasitoids, particularly those that emerged in the late larval stage or pupal stage, could cause a relatively high amount of mortality in endemic populations. Parry (1994) found that in Alberta *Carcelia malacosomae* (Sellers), *Leschenaultia exul* (Townsend) and *Aleiodes malacosomatos* (Mason) attacked larvae and pupae most frequently during the endemic phase of the cycle however, parasitism rates by *L. exul* were highly variable. Generally this parasitoid is recognized

as important during late stages of outbreaks (Witter and Kulman 1979). *Lespesia frenchi* (Williston) is also suggested to be an important mortality agent of endemic populations (Witter and Kulman 1979) however, in Alberta this parasitoid has not been frequently detected (Parry 1994). These parasitoids, in conjunction with generalist predators may help to slow the increase of innocuous FTC populations over time. Furthermore, generalist parasitoids and superparasitoids may be able to respond to increases in FTC populations by virtue of their diverse prey preferences and higher reproductive output compared to birds and ground beetles. Their ability to parasitize numerous species of prey ensures their presence within a system and theoretically allows for a relatively quick response to an increase in prey densities (Root 1973). Spatial variation in predation rates may also prolong the duration of endemic populations of FTC. Parry (1994) found that predators were able to respond quickly to local increases of FTC and generally exerted strong predation pressure within these small areas. Many other studies have shown that generalist predators are also able to respond to small local increases in prey densities (Elkinton *et al.* 2004; Schauber *et al.* 2004). It is unknown however, if these localized increases in FTC population density are characteristic of natural processes. There is evidence to suggest that this does not happen and that background densities gradually increase, relatively consistently, throughout a regional landscape, creating no 'hot spots' to which generalist predators may respond (J. Roland personal communication).

Vegetation complexity

Plot characteristics may alter movement of organisms within a habitat. For example, predator movement may be affected by differences in the amount of vegetation cover (Greenslade 1964; Pearsall and Walde 1995; Petit and Usher 1998) resulting in reduced efficiency of predators. There was no effect however, of percent herbaceous cover or shrub density on predation rates by any generalist predators. Pearce *et al.* (2003) found that stand type can influence the resident beetle community however species such as *Calosoma frigidum* and *Carabus serratus* have no strict association with stand type. Variability in abundance of some bird species can be partially explained by tree density (e.g. Shirley 2004). Predation of FTC was not affected however, by either tree density or the proportion of the forest stand comprised of aspen. The sites I used were relatively

similar in structure however, and small differences among them might have little effect on mortality of pupae.

Summary

Generalist predators, assumed to be mainly birds and beetles, impose a moderate level of mortality on populations of FTC pupae and their impact is additive. Although overall predation by generalist predators has a significant effect on FTC populations, it does not appear that they have the ability to regulate these populations. The fact that long intervals between FTC outbreaks do occur suggests that regulation of low density populations may occur via other mortality agents, perhaps in conjunction with generalist predators.

Interestingly, there was no effect of forest structure on predation by generalist predators, indicating that predator populations as a whole are equally effective in both forest structures. This suggests that predators are either always present in fragments or can move uninhibitedly through a heterogeneous landscape. There was however, evidence suggesting that predators consume a larger proportion of pupae in more distant fragments than in fragments close to continuous tracts of forest, which could be explained if foragers spend more time in more isolated patches to increase the energetic benefits obtained from these patches (Charnov 1976). Landscape configuration therefore seems to play a minor role in the relationships between forest-specialized predators and prey.

In conclusion, I determined that the predation by avian and beetle predators is additive and that the magnitude of predation is similar between forest structures. Furthermore, I determined that the combined response of all generalist predators to a gradient of FTC densities was most representative of a type II functional response described by Holling (1965). Of interest now, is whether these patterns of predation are observed for the individual guilds of predators, namely predators that obtain FTC pupae via climbing up into the canopy or predators that access pupae from above. These guilds are thought to be composed mainly of predatory beetles and birds, respectively. The following chapter will assess these two individual guilds' responses to changing background FTC densities,

fragmentation and landscape configuration. Additionally, predator populations may fluctuate between years, due to environmental conditions unrelated to FTC densities (Elkinton *et al.* 2004) which may in turn, affect the rates of predation exhibited by the individual guilds of predators. As such, I examine the relationship between bird or beetle abundance within plots, to their guilds' predation rates of FTC, is also assessed in Chapter 3.

LITERATURE CITED

Aune, K., B. G. Jonsson, and J. Moen. 2005. Isolation and edge effects among woodland key habitats in Sweden: is forest policy promoting fragmentation? *Biological Conservation* **124**:89-95.

Austen, M. J. W., C. M. Francis, D. M. Burke, and M. S. W. Bradstreet. 2001. Landscape context and fragmentation effects on forest birds in southern Ontario. *Condor* **103**:701-714.

Baur, B., A. Coray, N. Minoretti, and S. Zschokke. 2005. Dispersal of the endangered flightless beetle *Dorcadion fuliginator* (Coleoptera : Cerambycidae) in spatially realistic landscapes. *Biological Conservation* **124**:49-61.

Bayne, E. M. and K. A. Hobson. 2001a. Effects of habitat fragmentation on pairing success of ovenbirds: importance of male age and floater behavior. *Auk* **118**:380-388.

Bayne, E. M. and K. A. Hobson. 2001b. Movement patterns of adult male ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. *Condor* **103**:343-351.

Beaudry, S., L. C. Duchesne, and B. Cote. 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Canadian Journal of Forest Research* **27**:2065-2071.

Berryman, A. A., N. C. Stenseth, and A. S. Isaev. 1987. Natural regulation of herbivorous forest insect populations. *Oecologia* **71**:174-184.

Blomme, C. G. 1991. Ring-billed gulls, *Larus delawarensis*, feeding in flight on forest tent caterpillar, *Malacosoma disstria*, cocoons. *Canadian Field-Naturalist* **105**:280-281.

Brackenreed, A. 2000. Extensive defoliation in Alberta. *Alberta Environment Bugs and* Disease **11**:1-6.

Campbell, R. W. 1975. The gypsy moth and its natural enemies. USDA *Agricultural Information Bulletin* **381**.

Campbell, R. W. and T. R. Torgersen. 1982. Some effects of predaceous ants (Hymenoptera, Formicidae) on western spruce budworm (Lepidoptera, Tortricidae) pupae in North Central Washington. *Environmental Entomology* **11**:111-114.

Canadian Forest Service. 2001. Forest tent caterpillar. *Frontline Express, Great Lakes Forestry Centre Bulletin* **9**:1-2.

Case, T.J. 2000 An Illustrated Guide to Theoretical Ecology. Oxford University Press Inc. New York.

Celada, C. 2000. Territory choice and quality in the yellow warbler (*Dendroica petechia*). The importance of habitat spatial structure, spatial scale, social factors and the impact of cattle grazing. Ph.D. dissertation. University of Alberta, Alberta.

Charnov, E. L. 1976. Optimal foraging, marginal value theorem. *Theoretical Population Biology* **9**:129-136.

Clark, E. C. 1958. Ecology of the polyhedroses of tent caterpillars. *Ecology* **39**:132-139.

Crawford, H. S. and D. T. Jennings. 1989. Predation by birds on spruce budworm *Choristoneura fumiferana* - functional, numerical, and total responses. *Ecology* **70**:152-163.

Crins, W. J. 1980. 2 Aggregations of *Calosoma frigidum* (Coleoptera, Carabidae) in Ontario during 1976. *Entomological News* **91**:155-158.

Cronin, J. T. 2003. Movement and spatial population structure of a prairie planthopper. *Ecology* **84**:1179-1188.

Davis, S. K. 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. *Auk* **121**:1130-1145.

Desrochers, A. and M. J. Fortin. 2000. Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. *Oikos* **91**:376-384.

Desrochers, A. and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* **11**:1204-1210.

Elkinton, J. S., W. M. Healy, J. P. Buonaccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith, and A. M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* **77**:2332-2342.

Elkinton, J. S., A. M. Liebhold, and R. M. Muzika. 2004. Effects of alternative prey on predation by small mammals on gypsy moth pupae. *Population Ecology* **46**:171-178.

Floyd, T. 1996. Top-down impacts on creosotebush herbivores in a spatially and temporally complex environment. *Ecology* **77**:1544-1555.

Ginzburg, L. R. and D. E. Taneyhill. 1994. Population-cycles of forest Lepidoptera - a maternal effect hypothesis. *Journal of Animal Ecology* **63**:79-92.

Gould, J. R., J. S. Elkinton, and W. E. Wallner. 1990. Density-dependent suppression of experimentally created gypsy-moth, *Lymantria dispar* (Lepidoptera, Lymantriidae), populations by natural enemies. *Journal of Animal Ecology* **59**:213-233.

Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* **33**:301-310.

Grubb, T. C. and P. F. Doherty. 1999. On home-range gap-crossing. *Auk* **116**:618-628.

Halme, E. and J. Niemela. 1993. Carabid beetles in fragments of coniferous forest. *Annales Zoologici* Fennici **30**:17-30.

Hanski, I. 1990. Density dependence, regulation and variability in animal populations. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **330**:141-150.

Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151-162.

Hanski, I. and P. Parviainen. 1985. Cocoon predation by small mammals, and pine sawfly population-dynamics. *Oikos* **45**:125-136.

Hassell, M. P., J. H. Lawton, and J. R. Beddington. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. *Journal of Animal Ecology* **46**:249-262.

Hassell, M. P. and R. M. May. 1973. Stability in insect host-parasite models. *Journal of Animal Ecology* **42**:693-726.

Hildahl, V. W. A. R. 1960. Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hübner, and their effects on stands of trembling aspen in Manitoba and Saskatchewan. *Canadian Entomologist* **92**:199-209.

Hinsley, S. A. 2000. The costs of multiple patch use by birds. *Landscape Ecology* **15**:765-775.

Hodson, A. C. 1941. An ecological study of the forest tent caterpillar, *Malacosoma disstria* Hbn. *Minnesota Agricultural Experiment Station Technical Bulletin* **148**

Hodson, A. C. 1977. Some aspects of forest tent caterpillar population dynamics. *Minnesota Agricultural Experiment Station Technical Bulletin* **310**

Holling, C. S. 1965. The functional response of predators to prey density. *Memoirs of the Entomological Society of Canada* **45**:1-60.

Jones, G. A., K. E. Sieving, M. L. Avery, and R. L. Meagher. 2005. Parasitized and non-parasitized prey selectivity by an insectivorous bird. *Crop Protection* **24**:185-189.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator prey interactions. *Nature* **326**:388-390.

Koenig, W. D. and J. M. H. Knops. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. *Journal of Animal Ecology* **70**:609-620.

Krebs, C. J. 1989. Ecological Methodology. Harper & Row., New York.

Larochelle, A. 1990. The Food of Carabid Beetles (Colepptera: Carabidae, Including cicindelinae). Faberies Supplément 51-132.

Larsson, S., B. Ekbom, and C. Bjorkman. 2000. Influence of plant quality on pine sawfly population dynamics. *Oikos* **89**:440-450.

Liebhold, A. M., K. F. Raffa, and A. L. Diss. 2005. Forest type affects predation on gypsy moth pupae. *Agricultural and Forest Entomology* **7**:179-185.

Lindroth, C. H. 1. 1969. The Ground Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Opuscula Entomologica Supplementum. Part 1-6.

Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* **39**:487-494.

Oaten, A. and W. W. Murdoch. 1975. Functional response and stability in predator-prey systems. *American Naturalist* **109**:289-298.

Parry, D. 1995. Larval and pupal parasitism of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) in Alberta, Canada. *Canadian Entomologist* **127**:877-893.

Parry, D. 1994. The impact of predators and parasitoids on natural and experimentally created populations of forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). Masters Thesis, University of Alberta, Alberta.

Parry, D., J. R. Spence, and W. J. A. Volney. 1997. Responses of natural enemies to experimentally increased populations of the forest tent caterpillar, *Malacosoma disstria*. *Ecological Entomology* **22**:97-108.

Pearsall, I. A. and S. J. Walde. 1995. A comparison of epigaeic Coleoptera assemblages in organic, conventional, and abandoned orchards in Nova-Scotia, Canada. *Canadian Entomologist* **127**:641-658.

Pelech, S. and S. J. Hannon. 1995. Impact of tent caterpillar defoliation on the reproductive success of black-capped chickadees. *Condor* **97**:1071-1074.

Petit, S. and M. B. Usher. 1998. Biodiversity in agricultural landscapes: the ground beetle communities of woody uncultivated habitats. *Biodiversity and Conservation* **7**:1549-1561.

Rail, J. F., M. Darveau, A. Desrochers, and J. Huot. 1997. Territorial responses of boreal forest birds to habitat gaps. *Condor* **99**:976-980.

Ramse D.A. Biological control of the forest tent caterpillar, *Malacosoma disstria* Hbn., in North Dakota. Masters Thesis, North Dakota State University, South Dakota.

Raymond, B., A. Vanbergen, A. Watt, S. E. Hartley, J. S. Cory, and R. S. Hails. 2002. Escape from pupal predation as a potential cause of outbreaks of the winter moth, *Operophtera brumata*. *Oikos* **98**:219-228.

Roland, J. 1994. After the decline - what maintains low winter moth density after successful biological control? *Journal of Animal Ecology* **63**:392-398.

Roland J. 1990. Interaction of parasitism and predation in the decline of winter moth in Canada. Pages 289-302.*in* A.D. Watt, S.R. Leather, M.D. Hunter and N.A.C. Kidd, editors. Population Dynamics of Forest Insects. Intercept Publishers, Andover.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* **93**:25-30.

Roland, J., B. G. Mackey, and B. Cooke. 1998. Effects of climate and forest structure on duration of forest tent caterpillar outbreaks across central Ontario, Canada. *Canadian Entomologist* **130**:703-714.

Roland, J. and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**:710-713.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats - fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95-120.

Rossiter, M. 1994. Maternal effects hypothesis of herbivore outbreak. *Bioscience* **44**:752-763.

Roth, D. 2005. The effects of forest fragmentation on parasitoids of the forest tent caterpillar (*Malacosoma disstria*) Masters Thesis, University of Alberta, Alberta.

SAS Release 9.1 (2002) SAS Institute Inc., Cary, NC

Satterthwaite, F. E. 1946. An approximate distribution of estimates of variance components. *Biometrics Bulletin* **2**:110-114.

Schauber, E. M., R. S. Ostfeld, and C. G. Jones. 2004. Type 3 functional response of mice to gypsy moth pupae: is it stabilizing? *Oikos* **107**:592-602.

Sealy, S. G. 1979. Extralimital nesting of bay-breasted warblers - response to forest tent caterpillars. *Auk* **96**:600-603.

Sealy, S. G. 1980. Reproductive responses of northern orioles to a changing food supply. *Canadian Journal of Zoology* **58**:221-227.

Shirley, S. 2004. The influence of habitat diversity and structure on bird use of riparian buffer strips in coastal forests of British Columbia, Canada. *Canadian Journal of Forest Research* **34**:1499-1510.

Simpson, E. H. 1949. Measurement of diversity. *Nature* **163**:688.

Sippell, W. L. 1962 Outbreaks of the forest tent caterpillar *Malacosoma disstria* Hbn., a periodic defoliator of broadleafed trees in Ontario. *Canadian Entomologist* 94: 408-416.

Southwood, T. R. E. and H. N. Comins. 1976. Synoptic population model. *Journal of Animal Ecology* 45:949-965.

St. Clair, C. C. M. Bélisle. A. Desrocher. a. S. Hannon. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology* [online] **2**:13.

Stark, E. J. and J. D. Harper. 1982. Pupal mortality in forest tent caterpillar (Lepidoptera, Lasiocampidae) - causes and impact on populations in southwestern Alabama. *Environmental Entomology* **11**:1071-1077.

Takekawa, J. Y., E. O. Garton, and L. A. Langelier. 1982. Biological-control of forest insect outbreaks - the use of avian predators. *Transactions of the North American Wildlife and Natural Resources Conference* **47**:393-409.

Turchin P. 1995. Population regulation: old arguments and a new synthesis. Pages 19-40. *in* N. Cappuccino and PW Price, editors. Population Dynamics: New Approaches and Synthesis. Academic Press, San Diego, California.

Villard, M. A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *Auk* **115**:801-805.

Weed, C. M. 1900. The forest tent caterpillar. New Hampshire College *Agricultural Experiment Station Bulletin* **75**:107-132.

Weed C., M. 1899. The forest tent caterpillar. New Hampshire College *Agricultural experiment Station Bulletin* **64**:75-98.

Weseloh, R. M. 1988. Effects of microhabitat, time of day, and weather on predation of gypsy-moth larvae. *Oecologia* **77**:250-254.

Winfree, R., J. Dushoff, E. E. Crone, C. B. Schultz, R. V. Budny, N. M. Williams, and C. Kremen. 2005. Testing simple indices of habitat proximity. *American Naturalist* **165**:707-717.

Witter, J. A. 1979. Forest tent caterpillar (Lepidoptera, Lasiocampidae) in Minnesota - case history review. *Great Lakes Entomologist* **12**:191-197.

Witter, J., A. H. M. Kulman. 1972. A review of the parasites and predators of tent caterpillars (*Malacosoma* Spp.) in North America. *Minnesota Agriculture Experimental Station Technical Bulletin* **289**.

Witter, J.A., H.M. Kulman. 1979. The parasite complex of the forest tent caterpillar in northern Minnesota. *Environmental Entomology* **8**:723-731

Zabel, J. and T. Tscharntke. 1998. Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* **116**:419-425.

Chapter 3

Bird- and beetle-mediated predation of forest tent caterpillars (*Malacosoma disstria* Hübner) in a fragmented landscape.

INTRODUCTION

In Chapter 2, I showed that birds and beetles, together with some unaccounted for predation, exert moderately high predation pressure on innocuous populations of forest tent caterpillars (FTC). At higher densities of the prey however, total generalist predation decreased linearly, providing evidence for a type II functional response. Therefore there was little evidence for any overall regulatory effect by generalists. Similar results have been demonstrated for generalist predation of both gypsy moth (Elkinton *et al.* 2004) and winter moth (Raymond *et al.* 2002). For both moth species however, positive density-dependent predation has also been documented (Campbell 1975; Roland 1994; Schauber *et al.* 2004). These results depend on which developmental stage the prey is being depredated, the predators involved and the abundance of alternative food (Campbell and Sloan 1977; Elkinton *et al.* 2004; Holling 1965). Although generalist predators combined, did not appear to be capable of regulating populations of FTC, in this chapter I will describe the individual predation curves of birds and beetles along an FTC density gradient to estimate their functional responses. To obtain independent estimates of bird-type and beetle-type predation, cages were used to exclude either beetles or birds, respectively. The proportion of pupae scored as "bird"- or "beetle"-type predation within the respective treatments, was used to estimate the impact of the two guilds on populations of FTC.

Forest Fragmentation

Habitat fragmentation may decouple prey populations from their natural enemies, resulting in decreased rates of predation or parasitism in isolated habitat stands (Kareiva 1987; Roland 1993). In Chapter 2, I found that total predation by all generalist predators did not differ between isolated forest fragments and tracts of continuous forest. Birds and beetles may however, respond differently to fragmentation. In this chapter I examine the possibility that guild-specific predation rates differ between forest structures. There is evidence to suggest that large-scale habitat disturbance reduces the distribution and abundance of some species of forest birds at both the regional and local scale (Norton and Hannon 1997; Hobson and Bayne 2000; Robinson 1998; Wilcove 1985). Fragments may be perceived by birds, particularly 'area-sensitive' species (Villard 1998), as being of

marginal quality resulting in reduced mate pairing and reproduction (Bayne and Hobson 2001; Burke and Nol 1998; Ficken and Ficken 1966; Robinson 1998). Because nesting females and young are potentially less abundant in fragments, predation on FTC may be reduced.

Effects of fragmentation on beetle populations are variable and species-specific (e.g. Halme and Niemela 1993; Lassau *et al.* 2005; Pearce *et al.* 2003). In general, species composition and abundance of forest carabids tend to be lower in fragmented forest stands (Halme and Niemela 1993; Vanbergen *et al.* 2005). The persistence of forest beetle fauna in isolated patches is dependent on interspecific interactions, suitability of habitat, and species' re-colonization ability (Barbaro *et al.* 2005; Beaudry *et al.* 1997; Burke and Goulet 1998; Driscoll and Weir 2005; Halme and Niemela 1993; Petit and Usher 1998). Moreover, strict forest specialists are often found only in large continuous forest tracts indicating that fragments are not simply samples of contiguous habitats (Halme and Niemela 1993). Fragmentation therefore, may lower FTC beetle predator abundance, causing decreased rates of beetle-mediated predation.

Predator Movement

Landscape configuration may differentially impede the movement of predator guilds and thus, patterns of predation among fragments may be related to fragment size, connectedness and isolation distance (Winfree *et al.* 2005). In Chapter 2, I showed that patch size and connectedness did not influence overall predation rates by all predators combined but that there was an increase in predation as patch isolation distance increased. In this chapter, I assess bird and beetle predation separately among fragments differing in size, connectedness and isolation distance.

Numerical response by birds and beetles

In Chapter 2, mortality agents, other than birds and beetles were no doubt present and thus the numerical responses of these predators could be obscured. Since the numerical response by generalist predators, combined with their functional responses, determines their importance in the regulation of forest insect populations, this chapter addresses the separate numerical responses of the two predator guilds, based on surveys estimating

predator abundances. These measures are then related to guild-specific predation by both bird or beetle predators.

This chapter follows Chapter 2 by examining guild-specific predation rates rather than total mortality, and addresses how generalist predator communities may change in response to prey outbreaks. The objectives are to 1) describe the separate shapes of the bird and beetle predation curves along a gradient of prey density, 2) determine if the separate predation rates by these two guilds are negatively affected by forest fragmentation 3) determine whether landscape configuration alters predation pressures by birds or beetles differently, 4) assess predation rates in light of predator abundance and diversity, and 5) determine whether generalist predators of FTC exhibit a numerical response to FTC outbreaks.

METHODS

Study Regions

Bird and beetle predation rates on FTC pupae were assessed during the summers of 2003 and 2004. Experiments were conducted within two regions in central Alberta, Canada. The Rocky Mountain House Provincial Grazing Reserve region ('*Rocky*') is found within the mixed wood forests of Alberta located approximately 200 km southwest of Edmonton, Alberta and had moderately high to very high densities of FTC during the years of study. The Black Bear Provincial Grazing reserve ('*Black Bear*') is located 150 km north of Edmonton (Fig. 2.1). Populations of forest tent caterpillar have been relatively low since 1990 but appear to be increasing (Roland unpublished data). For a more complete description of regional characteristics, see Chapter 2.

Experimental design

The experimental design is basically that described in Chapter two with one main difference; within each plot, an independent estimate of bird-type or beetle-type predation was recorded rather than an estimate of total predation.

Bird-specific and beetle specific predation

In both years, once moths emerged from the cocoons, I collected the planted pupae in "blind" labeled bags. In the lab, cocoons and pupae were examined for evidence of either bird or beetle predation. Bird predation was identified by the presence of a large, clean tear in the inner and outer layer of the cocoon and the complete disappearance of the pupa within (Fig. 3.1). In contrast, beetle predation was identified by the presence of small jagged tears in both the outer and inner layers of the cocoon and the presence of a shredded pupal casing (Fig. 3.2). Evidence of parasitism can be similar to beetle predation however, the pupal case is generally not shredded instead there is either a small clean emergence hole on the casing or there is a live fly or wasp larva within the pupal casing.

Bird predation rates were calculated by dividing the number of pupae consumed by only birds by the number of pupae planted on trees from which beetles were excluded:

$$\text{Proportion pupae consumed by birds} = \frac{\text{number pupae preyed on by birds}}{\text{number pupae initially planted on tree}}$$

Beetle predation rates were calculated by dividing the number of pupae with beetle-type predation by the number of pupae planted on trees from which birds were excluded.

$$\text{Proportion pupae consumed beetles} = \frac{\text{number pupae preyed on by beetles}}{\text{number pupae initially planted on tree}}$$

In both cases a more conservative and precise estimate of predation by each guild was obtained compared to that used in the analysis in Chapter 2.

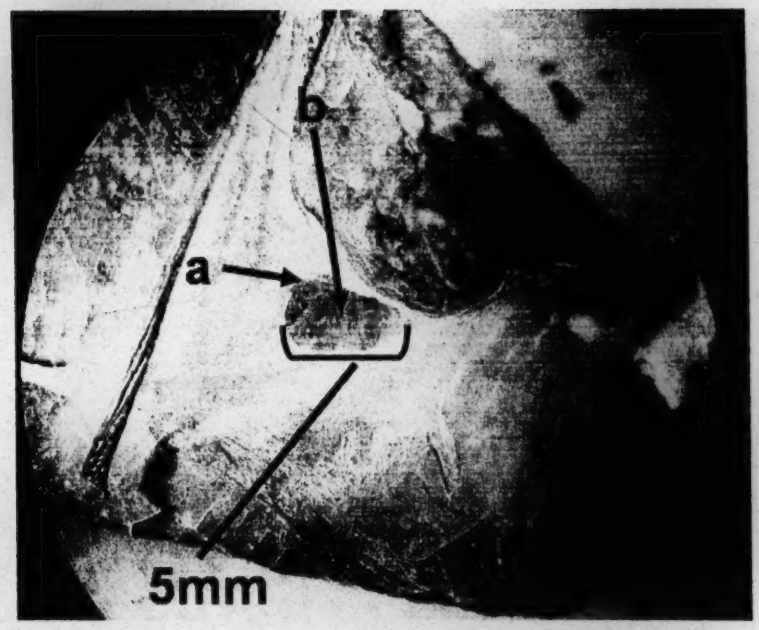

Figure 3.1. Example of bird type predation characterized by (a) a 'clean' tear in the cocoon and (b) the complete removal of the pupa.

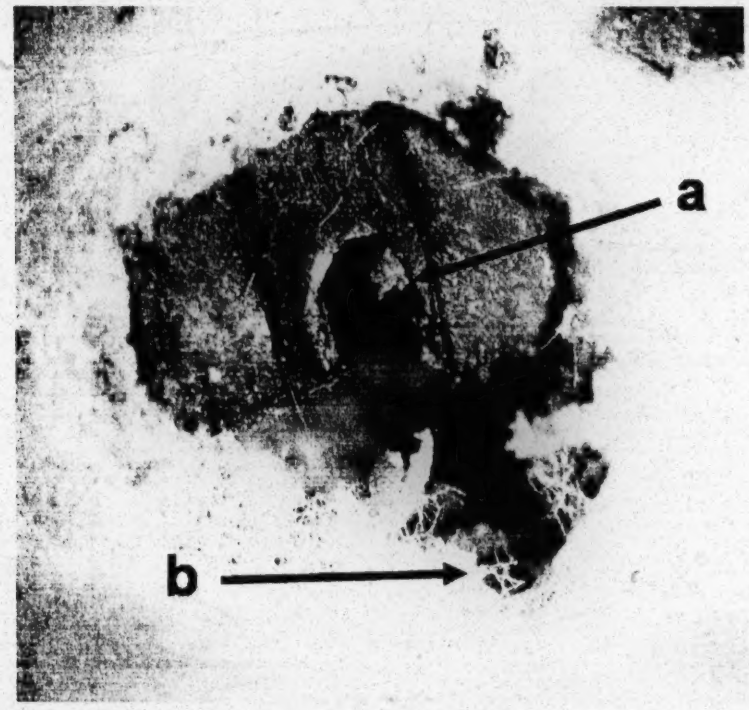

Figure 3.2. Example of beetle type predation characterized by the presence of (a) the pupal casing and (b) the shredded cocoon.

Pupal abundance, landscape configuration and plot characteristics

I estimated the abundance of pupae in each plot using the methods described in Chapter 2. Furthermore, the methods used to determine landscape configuration and plot vegetation characteristics are also described in Chapter 2 and applied to this chapter.

Predator community

Bird surveys were conducted in both years to estimate the abundance and diversity of bird predators within each of the forest fragments and continuous forest tracts. One point count station in each of the forest patches was located between the beetle-exclusion and bird-exclusion trees. All birds within a 50m fixed radius were recorded once a season, over a 10 minute period. Because forest fragments were sometimes less than 1ha in size, grassland birds singing in the area surrounding the isolated forest patch were also recorded. If grassland birds were heard within the 50m fixed radius in continuous forests, they were also recorded. Counts were conducted between sunrise and 8:30am MDT but were not done during periods of rain or when winds were greater than three on the Beaufort scale. In both years the double-observer approach was used to increase the probability of detection and to reduce variation between surveys (Nichols *et al.* 2000). In 2003 the same two individuals conducted surveys in all the fragments and another pair conducted surveys in all the continuous tracts. In 2004, all plots were surveyed by the same pair of individuals. It is unlikely that individual birds were counted twice in different sites because they are all separated by at least one kilometer. Individual birds may have been recorded in both a fragment and its paired continuous tract, but for the purposes of this study it is assumed there was little movement between paired patches. I excluded individuals that flew over the patch because it was unknown whether they used the patch or not.

The total number of birds and total number of bird FTC predators per plot (predators listed in Appendix A) was determined for each plot in each year. There are numerous documented bird and beetle predators of FTC. However, there is little information on their prey preferences in terms of the developmental stages of FTC. In addition, the presence of a specific predator in plots may be influenced by the presence of early, as

well as late stage larvae and pupae. Since the information on bird predators of FTC pupae is limited and the number of birds that are recorded as pupal predators within each plot was very low, I included all known avian predators of FTC in my analyses, regardless of whether they have only been recorded as depredating eggs, larvae or pupae.

Beetle predator abundance was estimated in 2004 using pit fall traps. Plastic containers (750mL) with an upper rim of 11cm diameter were used because they are capable of trapping larger bodied carabid beetles (Work *et al.* 2002). Five traps were embedded in the soil along a 50m transect between the bird and beetle exclusion treatments in each plot. Each trap was 10m from the next trap. Each container contained 100ml of glycerol-free antifreeze (Motormaster brand). I did not cover traps to prevent debris from entering them but instead monitored them approximately twice a week and replaced them if destroyed or filled with debris. Traps were set out during the week prior to FTC pupation and the final collection was done once all adult FTC moths had emerged and the planted pupae had been collected. Samples were preserved in 70% ethanol and returned to the lab for identification at the Strickland Entomological Museum at the University of Alberta. I identified only beetles belonging to the genus *Calosoma*, *Scaphinotus*, *Carabus* and *Pterostichus* as they are documented as being potential predators of FTC (Appendix B). Because there were so few predators trapped, the number of beetle predators within each plot was summed. Beetle larvae were not considered in this experiment although they are known to be important predators of other forest Lepidoptera (Larochelle 1990).

ANALYSIS

Analyses were conducted separately for bird and beetle predation rates to determine the effects of forest structure, FTC density and year. In some cases, the experimental tree fell over or was otherwise destroyed, in which case the data point was omitted prior to analysis. All data were analyzed using procedures in SAS (SAS Inst. Inc. v.9.1 2002). When appropriate, proportions were arcsine square-root transformed to stabilize variances. Results were considered significant with a P-value ≤ 0.05. Because it was

not reasonable to assume that the populations have equal variances, I used the Satterthwaite approximation of degrees of freedom for all mixed model procedures.

Main effects: forest structure, prey density, year

To assess the effects of the experimental treatments on predation by birds, data were analyzed using a repeated measures, mixed model procedure in SAS (PROC MIXED). To control of the different methods of pupal deployment between years, YEAR was added as a fixed effect. STRUCTURE and background FTC DENSITY were included as fixed factors because their effects on predation were of particular interest. To control for differences in predation rates between regions (Rocky and Black Bear) and sites, where the paired forest types were located, I blocked SITE, nested within REGION. These terms were added as random factors because their effects on predation rates are not of specific interest. The same analysis was performed for predation by beetles.

Pattern of predation across the range of FTC densities

I assessed the potential for non-linear effects of density on residual predation by birds and by beetles separately. Residual predation was obtained from the above repeated measure, mixed model analyses, except that the DENSITY term was omitted. A General Linear Model (GLM) was used to assess the effect of adding either a quadratic or cubic density term to the model (Elkinton *et al.* 2004). The resulting pattern was used as the basis on which to infer the possible functional response by each guild.

Landscape characteristics – predation among fragments

I assessed the effect of landscape configuration using the residual mortality bird predation estimated among fragments. Residual bird predation was obtained from the main effects repeated measures analysis in the first section, in which, STRUCTURE, DENSITY and YEAR were fixed factors. The effect of the SIZE of the isolated patch, the DISTANCE of the patch to the nearest continuous forest tract and the CONNECTEDNESS of the surrounding landscape were examined independently using the GLM procedure in SAS (PROC GLM). Non-linear relationships between residual morality and the patch measures were assessed with a non-parametric spline fit using the Generalized Additive

Model procedure in SAS (PROC GAM). The same analysis was to assess the effects of landscape characteristics on beetle-mediated predation.

Plot characteristics

The effects of plot vegetation on bird-mediated and beetle-mediated predation rates were assessed, again using the residual mortality from the main factor analysis, and using the GLM procedure in SAS (PROC GLM), I examined the linear relationships with vegetation. Vegetation variables were: density of aspen tree, the absolute number of trees per hectare, diversity of trees in each plot, the relative proportion of herbaceous cover in each plot, and the density of shrub vegetation greater than 0.3m. Non-linear trends were assessed using a Generalized Additive Model (PROC GAM) in SAS and fitting a non-parametric spline. These procedures were assessed separately for predation by birds and by beetles.

Predator abundance

To determine whether bird predators exhibited a numerical response to increased FTC density, I assessed the effect of FTC DENSITY on bird predator abundance by using the repeated measures mixed model procedure in SAS. BIRD PREDATOR abundance within a 50m radius was assessed using the GLM procedure (PROC GLM). The response variable again is the residual mortality of pupae inflicted by birds, after controlling for forest STRUCTURE, background FTC DENSITY, and YEAR. Since predator abundance may itself be affected by forest structure and may vary annually, I evaluated the effects of both STRUCTURE and YEAR on FTC bird predator abundance.

The effect of BEETLE PREDATOR abundance was assessed against residual predation rates among trees in which birds were excluded in 2004, using a General Linear Model (PROC GLM). The residual mortality was obtained from the primary factor analysis of predation rates exhibited by beetles, and for which STRUCTURE, FTC DENSITY, and YEAR were accounted for. I did not examine the effect of either beetle species richness, diversity or total beetle abundance because only known predator species were identified and counted from the pitfall traps. In addition, very few individual predators were

trapped in either forest structure or in either region, thus my confidence in correlating beetle predation with species richness or diversity is limited. Furthermore, pit fall trapping tends to capture individuals that are active and that are less affected by vegetation cover (Greenslade 1964). Thus, for the purposes of this study, it is inappropriate to analyze residual predation rates in relation to beetle diversity. For the same reasons, numerical response of beetle predators was not assessed.

RESULTS

Main effects: year, structure and density

Year- The average percentage of pupae scored as bird type predation collected from trees in which beetles were removed was 18% and 6%, in 2003 and 2004 respectively. The percentage scored as beetle-type predation on trees that excluded birds was 16% and 25% respectively (Fig 3.3). These rates did not differ significantly between years (Table 3.1), after controlling for STRUCTURE, DENSITY and SITE nested within REGION.

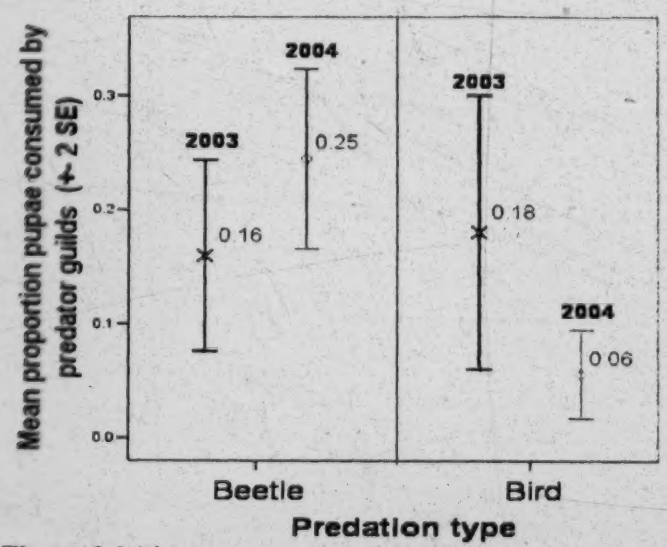

Figure 3.3 The average proportion of pupae scored as bird or beetle type predation in 2003 and 2004. Bars denote two standard errors of the mean.

Table 3.1. Test of fixed effects on rates of predation by avian predators and beetle predators on forest tent caterpillar pupae in 2003 and 2004.

Parameter	Numerator df	Denominator df	F-value	P-value
Bird predation				
YEAR	1	27.2	2.47	0.13
STRUCTURE	1	23.8	0.45	0.51
DENSITY	1	32.2	0.71	0.41
YEAR x STRUCTURE	1	27.2	0.16	0.69
STRUCTURE x DENSITY	1	32.2	0.05	0.82
Beetle predation				
YEAR	1	27	2.02	0.17
STRUCTURE	1	24	0.02	0.90
DENSITY	1	36.8	1.15	0.28
YEAR x STRUCTURE	1	27	0.57	0.46
STRUCTURE x DENSITY	1	36.8	0.56	0.46

Structure - The proportion of pupae consumed by birds in beetle excluded cages did not differ significantly between continuous forest patches and forest fragments (Table 3.1). In 2003, birds consumed on average 22% of the planted pupae in continuous forest tracts and 14% in isolated stands. In 2004, birds consumed 6% of pupae in both continuous forest and isolated stands (Fig. 3.4). Similarly, beetle-type predation rates on trees in which birds were excluded did not differ significantly between forest structures (Table 3.1). In both 2003 and 2004, predation rates in continuous forest stands averaged 21%. In 2003, the average predation rates in isolated patches were lower in isolated patches, at 11%, but increased to 28% in these same fragments in 2004 (Fig. 3.5).

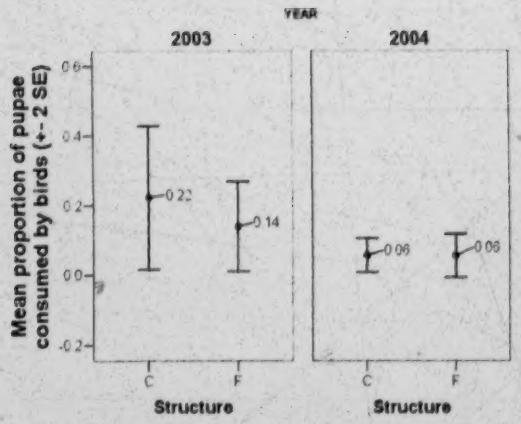

Figure 3.4. The average proportion of pupae scored as *bird-type* predation on trees from which beetles were excluded in continuous forest tracts and isolated forest fragments, in 2003 and 2004. Bars denote two standard errors of the mean.

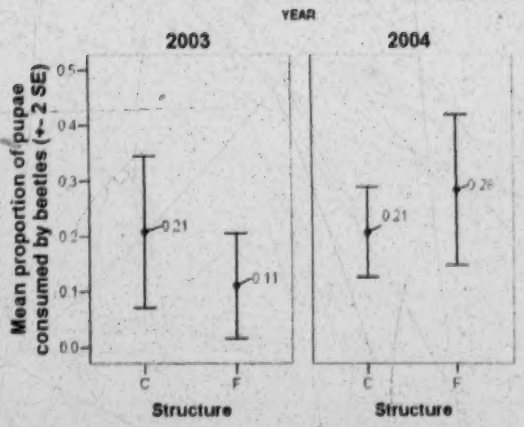

Figure 3.5. The average proportion of pupae scored as *beetle-type* predation on trees from which birds were excluded in continuous forest tracts and isolated forest fragments in 2003 and 2004. Bars denote two standard errors of the mean.

FTC density - Both bird-type and beetle-type predation rates decreased linearly as background density of FTC increased over the two years (Fig. 3.6 and 3.7) however, neither of these relationships were significant (Table 3.1). Furthermore, there were no significant nonlinear effects of prey density on predation rates by birds or beetles (Tables 3.2 and 3.3) after controlling for SITE, REGION, STRUCTURE and YEAR.

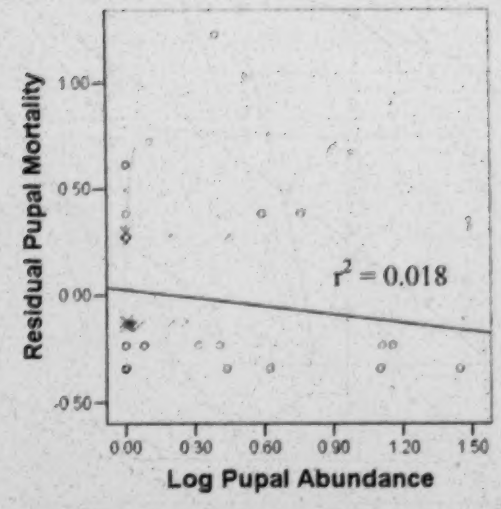

Figure 3.6. The residual mortality of forest tent caterpillar pupae depredated by birds, as a function of pupal density in 2003 (o) and 2004 (x) (P = 0.41).

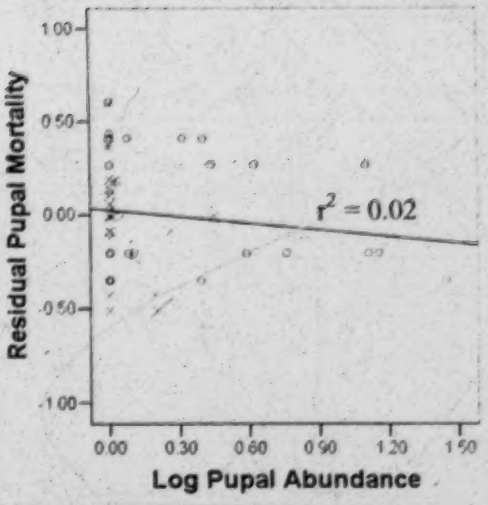

Figure 3.7. The residual mortality of forest tent caterpillar pupae depredated by beetles, as a function of pupal density in 2003 (o) and 2004 (x) (P = 0.28).

Table 3.2. The effect of prey density on *bird-type* predation. Parameter estimates are obtained from linear and non-linear fit models of residual predation after controlling for forest structure and year in 2003 and 2004

Parameter	Estimate	SE	Probability of > t
Linear Model			
b_0	0.026	0.058	0.65
b_1	-0.128	0.141	0.37
Quadratic Model			
b_0	-0.007	0.06	0.90
b_1	0.51	0.43	0.24
b_2	-0.58	0.37	0.12
Cubic Model			
b_0	-0.01	0.06	0.87
b_1	0.72	0.92	0.44
b_2	-1.06	1.99	0.60
b_3	0.25	1.96	0.81

Table 3.3. The effect of prey density on *beetle-type* predation. Parameter estimates are obtained from linear and non-linear fit models of residual predation after controlling for forest structure and year in 2003 and 2004

Parameter	Estimate	SE	Probability of > t
Linear Model			
b_0	0.024	0.050	0.63
b_1	-0.119	0.122	0.34
Quadratic Model			
b_0	0.014	0.054	0.79
b_1	0.076	0.381	0.84
b_2	-0.175	0.324	0.59
Cubic Model			
b_0	0.023	0.056	0.68
b_1	-0.440	0.814	0.59
b_2	1.066	1.757	0.54
b_3	-0.655	0.911	0.48

Landscape Structure

Patch size: The size of isolated forest patches in the *Black Bear* and *Rocky* regions, varied from 0.675 ha to 13.41 ha. There was no significant linear nor non-linear effect of PATCH SIZE on predation by birds after controlling for STRUCTURE, DENSITY and YEAR (Table 3.4). Similarly, there was no linear effect of PATCH SIZE on predation by beetle predators, after controlling for main effects (Table 3.5). There was however, a non-linear effect of patch size on beetle predation (Table 3.5; Fig. 3.8) as indicated by the spline smoother, however, neither the quadratic nor the cubic model were significant and the nonlinear relationship was not investigated further (Quadratic model: $F_{2, 21} = 0.31$, $P = 0.74$; Cubic model: $F_{3, 20} = 1.77$, $P = 0.19$).

Isolation distance: Density of FTC was negatively related to the DISTANCE of the isolated patch from the continuous forest tract in both years (2003: $P = 0.037$, correlation coefficient = -0.301; 2004: $P = 0.029$, correlation coefficient = -0.316). Because of this confounding effect, I removed density from the main model and used the resulting residual predation to assess the effect of isolation DISTANCE on predation by each of

the guilds of predators among fragments. The distances of isolated forest patches to the nearest continuous forest tracts ranged from 105m to 390m (mean = 250m). On average, these distances were shorter at *Rocky* (192.5m) than at *Black Bear* (275m). There were no significant linear or non-linear effects of DISTANCE on predation by birds (Table 3.4). Similarly, there was no linear effect of DISTANCE on predation by beetle. There was however, a weak non-linear trend (P = 0.07) of increasing beetle predation as DISTANCE increased from 100m to 275m but then decreased at greater distances (Fig. 3.9; Table 3.5). However, neither the quadratic nor the cubic models sufficiently explained more of the variation in beetle-mediated predation (Quadratic model: $F_{2, 21} = 1.35$, P = 0.28; Cubic model: $F_{3, 20} = 0.97$, P = 0.43).

Connectedness: There were neither linear, nor non-linear effects of connectedness on predation inflicted by either guild of predator (Table 3.4 and 3.5) indicating equal accessibility by both predators.

Table 3.4. Linear and non-linear effects of landscape characteristics of forest fragments on the proportion pupae consumed by bird predators (both summers combined).

Variable	$F_{1, 22}$	Linear Effect P-value	X^2	Non-linear Effect (Spline)
Patch size (m^2)	2.13	0.16	3.42	0.33
Distance*	0.73	0.40	0.40	0.94
Connectedness	0.01	0.91	3.98	0.26

**Distance of fragment to nearest continuous forest tract*

Table 3.5. Linear and non-linear effects of landscape characteristics of forest fragments on the proportion pupae consumed by beetle predators (both summers combined).

Variable	$F_{1, 22}$	Linear Effect P-value	X^2	Non-linear Effect (Spline)
Patch size (m^2)	0.11	0.75	11.26	0.01
Distance*	0.20	0.66	7.21	0.07
Connectedness	0.37	0.25	4.87	0.18

**Distance of fragment to nearest continuous forest tract*

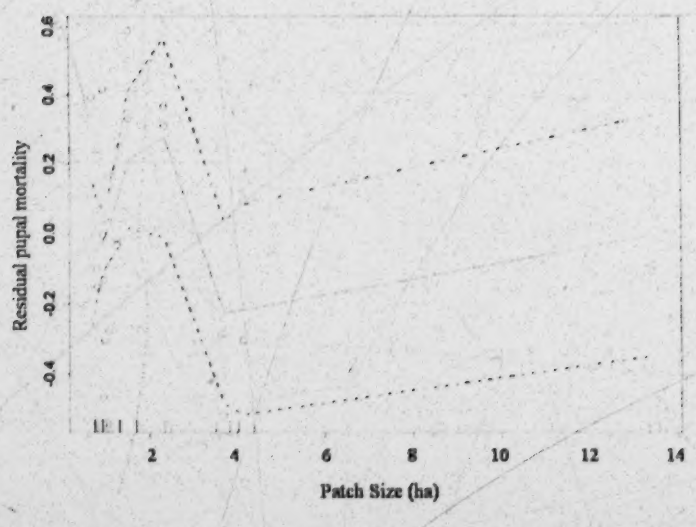

Figure. 3.8. Residual beetle predation as a function of patch size fit with a non-linear spline smoother after controlling for year, structure, and prey density (P = 0.01) (dashed line: 1 standard error).

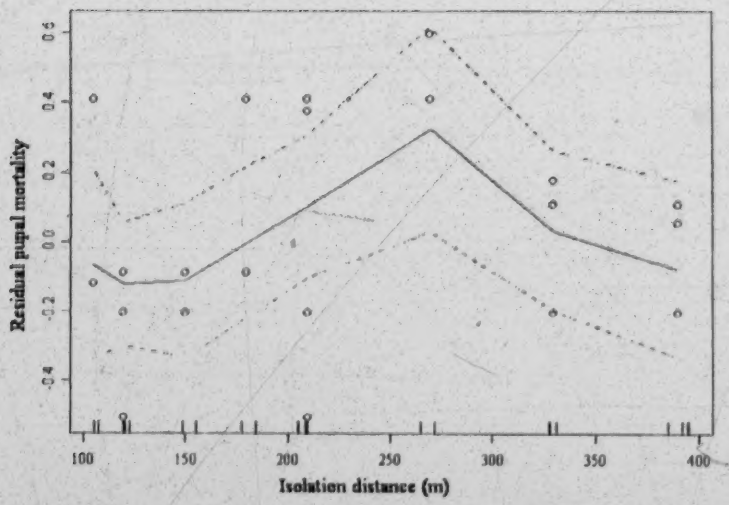

Figure. 3.9. Residual beetle predation as a function of patch isolation distance from the nearest tract of continuous forest, fit with a spline smoother after controlling for year, forest structure and prey density (P = 0.07) (dashed line:1 standard error).

Site Vegetation Characteristics

There were no effects of aspen density or absolute tree density on bird or beetle mediated predation rates (Tables 3.6 and 3.7). Similarly, predation by either predator guild was not affected by tree diversity or shrub density. There was no linear effect of herbaceous cover on bird-mediated predation of FTC pupae but there was a weak trend of lower beetle-mediated predation in those plots having higher proportion of herbaceous ground coverage (Fig. 3.10).

Table 3.6. The effects of vegetation characteristics on residual bird predation of forest tent caterpillar pupae over two years. Residual predation was obtained from the main effects model.

Variable	$F_{1, 45}$	P value
Bird predation		
Number aspen per hectare	0.04	0.83
Absolute number of trees per hectare	0.08	0.78
Simpson's tree diversity	0.60	0.44
Proportion ground cover*	1.12	0.30
Shrub vegetation density (plants/m2)	0.60	0.44

**Proportion ground covered with herbaceous vegetation*

Table 3.7. The effects of vegetation characteristics on residual beetle predation forest tent caterpillar pupae over two summers. Residual predation was obtained from the main effects model.

Variable	$F_{1, 46}$	P value
Beetle predation		
Number aspen per hectare	0.61	0.44
Absolute tree density per hectare	0.21	0.65
Simpson's tree diversity	1.59	0.21
Proportion ground cover*	2.59	*0.11*
Shrub vegetation density (plants/m2)	0.30	0.82

**Proportion ground covered with herbaceous vegetation*

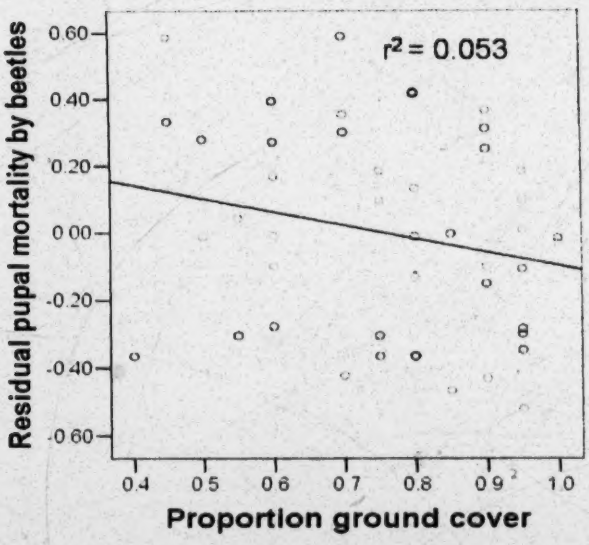

Figure 3.10. Residual predation rates of FTC pupae exhibited by beetle predators with increasing vegetation cover, after controlling for year, forest structure and prey density (P = 0.11).

Predator abundance

Between 2003 and 2004, the average number of documented BIRD PREDATORS in each region increased significantly from 3.33 birds to 6.58 birds per plot (Table 3.6; Fig 3.11). The abundance of BIRD PREDATORS did not differ between forest structures (Table 3.6; Fig 3.12), nor was there any evidence of a numerical response of bird predators as abundance of bird predators did not increase significantly with increasing FTC densities (Table 3.6). Appendix A lists the known bird predators found in the Rocky and Black Bear regions, over the two years of study.

Table 3.6: Repeated measures analysis of the main treatment effects on predatory bird abundance in 2003 and 2004.

Parameter	Numerator df	Denominator df	F-value	P-value
YEAR	1	26.8	27.84	< 0.0001
STRUCTURE	1	20.3	0.00	0.98
DENSITY	1	34.9	1.54	0.22
YEAR x STRUCTURE	1	20.8	0.11	0.74

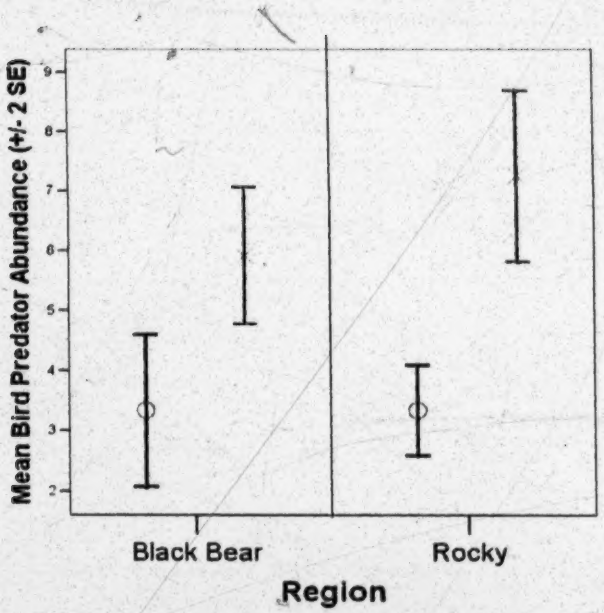

Figure 3.11. The abundance of avian predators of forest tent caterpillars in 2003 (o) and 2004 (x), in the Black Bear and Rocky regions. Bars denote two standard errors of the mean.

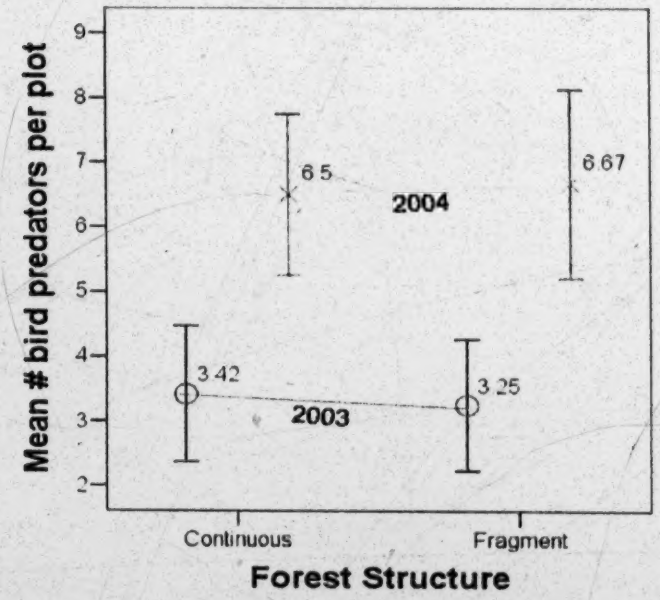

Figure 3.12. The average number of avian predators (+/- 2 standard errors) in continuous forest tracts and isolated forest stands in 2003 (o) and 2004 (x). Bars denote two standard errors of the mean.

Although there was no effect of density of FTC pupae on the abundance of bird predators, I did examine the relationship between bird abundance and bird-type predation. Using residual mortality, after controlling for YEAR, FTC DENSITY and forest STRUCTURE, the abundance of predatory birds was not related to predation rates (GLM; $F_{1,46} = 0.47$, $P = 0.50$. Interestingly, the Baltimore oriole (*Icterus galbula*), although recorded in the *Rocky* region in both years, did not show an aggregative response to high FTC abundances, as reported by other authors (Parry 1994; Sealy 1980). There were only seven orioles recorded over the two years of study, all of which were found at one site. Interestingly, this site had the second-highest FTC density in the study over the two years.

Beetle predators were trapped only in 2004. A total of 123 carabid predators were trapped across all sites over the three week period. Of the 123 beetles collected, 94 were *Pterostichus melanarius,* 34 of which were trapped in the isolated fragment of site 6 and 54 trapped in the continuous forest tract of the same site in the *Rocky* region. In both 2003 and 2004, this site had consistently the highest densities of FTC pupae. The other 29 beetles belonged to genus *Calosoma* (*C. frigidum, C. monoliatum* and *C. calidum*), *Carabus* (*C. chamissonis, C. taedatus* and *C. serratus*) and *Scaphinotus* (*S. marginatus*). After accounting for FTC density and forest structure, predation rates decreased significantly with increasing beetle abundance (log transformed) ($F_{1,22} = 5.10$, $P = 0.034$; Fig.3.13). Because *P. melanarius* was dramatically higher at site 6, I also examined the relationship without *P. melanarius*; there was no significant effect of beetle predator abundance on predation ($F_{1,22} = 0.78$, $P = 0.39$; Fig.3.14).

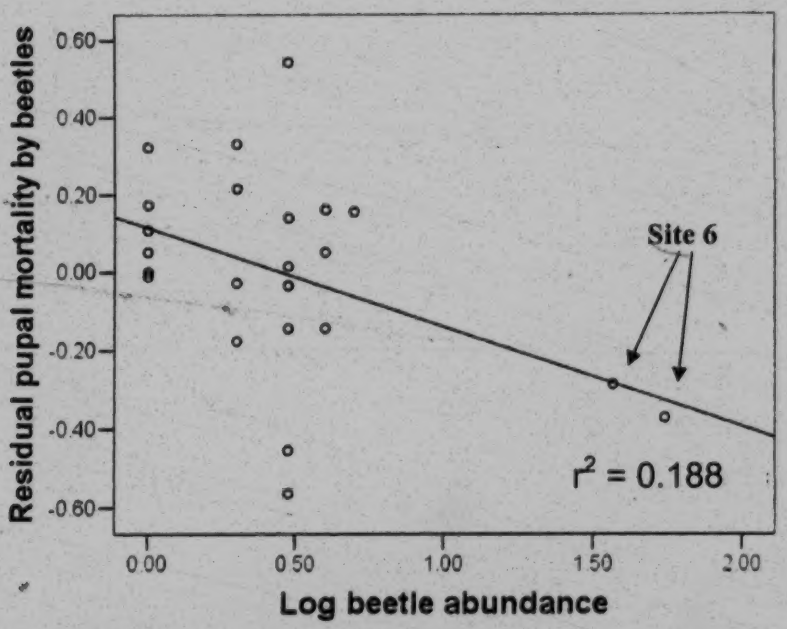

Figure 3.13. The residual mortality of FTC pupae with increasing beetle abundance including *P. melanarius* (P = 0.034).

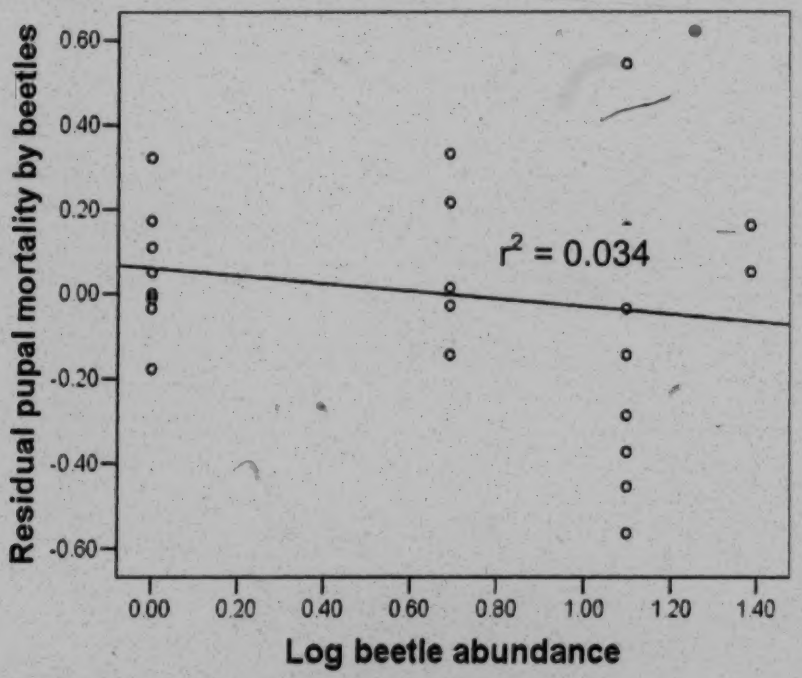

Figure 3.14. The residual mortality of FTC pupae with increasing beetle abundance, excluding *P. melanarius* (P = 0.39).

DISCUSSION

Overview

Results in Chapter 2 were based on predation by all generalist predators combined and I found that predators exhibited inversely density-dependent predation across a range of naturally occurring FTC densities. Furthermore, rates of generalist predation did not differ between forest structures although there was a trend of increasing predation as fragment isolation distance increased. In the current chapter, I examine the same relationships but did so on an individual predator-guild basis to determine whether either of the individual guild patterns of predation differs from those observed for all predators. Thus, the response variable used in this chapter is different from that in Chapter 2 in that it is only the predation confirmed to be either bird- or beetle-inflicted. Independent estimates of guild-specific predation rates, in the absence of other predators, were imperative to address the questions in this chapter. Although this methodology ensured independent estimates of guild-specific predation, as a caveat, it also reduced the number of samples that could be used to assess the relationships.

Experimental Treatments

Bird Predation: Avian predators are capable of exerting strong predation pressure on low density populations of forest insects (Crawford and Jennings 1989; Holling 1965; Morris *et al.* 1958; Parry 1994). There are approximately 60 documented avian predators of the tent caterpillar (Witter and Kulman 1972) although it is likely that many more insectivorous bird species will feed on at least one of the life stages of FTC. Parry (1994) found that in central Alberta, avian predation on FTC increased at the onset of the fifth larval instar developmental stage and remained high through pupation. He suggested that this increase coincided with the nesting phase of breeding songbirds of the region. Similar timing was observed in my plots in that birds were still exhibiting territorial behaviour during the FTC pupal stage. Furthermore, Parry (1994) reported that birds accounted for 90% of FTC mortality in his experimental plots. In contrast, the bird-mediated predation rates observed in the present study were much lower at approximately 18% mortality in the first year and dropping to 6% in the second year. Parry (1994)

however, increased naturally low FTC densities artificially, to outbreak levels over a small spatial scale. The birds in his experiment may therefore have responded to the small-scale local increases in prey abundance, and inflicted unusually high predation rates.

Parry (1994) reported that Baltimore orioles (*I. galbula*) are particularly important mortality agents of FTC larvae and pupae. Similarly, Sealy (1980) found that orioles exhibited an aggregative response to a naturally occurring FTC outbreak in Manitoba, however; the regional extent of that outbreak is unknown. In the present study, seven orioles were recorded over the two years, and only in the *Rocky* region. The lack of an aggregative response to the high FTC densities in my study may be related to the large spatial extent of the outbreak.

Beetle predation - Although there are numerous arthropod predators of FTC larvae and pupae (Larochelle 1990; Witter and Kulman 1972) there have not been any quantitative estimates of their effects on FTC populations. I assumed that most beetle-type predation was caused by *Calosoma* beetles, particularly *C. frigidum* since these beetles are known to climb trees to access larvae and pupae (Parry 1994; Witter and Kulman 1979). Peak activity of *C. frigidum* in southern Ontario occurs in June and decreases in early July (Crins 1980). In central Alberta however, peak activity may occur later due to lower spring and summer temperatures, which would coincide well with late larval and pupal stages of FTC. *Calosoma frigidum* were in fact trapped in both regions in 2004, during FTC pupation. Beetle-mediated predation rates were relatively constant in both years and were higher than bird predation. These results differ from Parry (1994) who found that birds consumed approximately 90% of deployed pupae from his plots, substantially more than beetle predators. Beetle predation however, may have been lower in his plots because highly mobile birds were likely responding to small-scale, artificial outbreaks whereas less mobile beetles would not. Furthermore, Parry (1994) did not specifically distinguish between bird- and beetle-type predation and may therefore, have lumped these two sources of mortality together thus inflating bird-type predation estimates.

Forest fragmentation and avian-mediated predation of FTC

Forest songbirds may be less abundant in forest fragments (Doherty and Grubb 2002; Hannon and Schmiegelow 2002) because of altered the food supply (Burke and Nol 1998), increased nest predation along edges and in fragments (Andren 1992; Wilcove 1985), reduced pairing success of area-sensitive birds (Bayne and Hobson 2001a), and/or altered movement patterns of birds within the landscape (Desrochers and Hannon 1997; Rail *et al.* 1997). These effects of fragmentation on birds were expected to be reflected in lower predation rates of FTC pupae in isolated fragments. The absence of such an effect suggests that bird predators of FTC establish feeding territories within fragments as frequently as they do in continuous tracts of forest or that their movement for foraging is not impeded by landscape fragmentation, at least not at the scale used in this study.

Bird predator abundance was similar in both forest structures, which may explain the similarity in predation between the two. Bird populations are often negatively affected by edge effects (Bayne and Hobson 2001a; Burke and Nol 1998; Rail et al. 1997; Wilcove 1985), up to 150m into the forest interior (Aquilani and Brewer 2004). Since the continuous forest plots were all located near forest edges, birds in isolated fragments and continuous forest plots likely experienced similar rates of nest predation and food availability (e.g. Celado 2000). It is plausible therefore, that the similar forest conditions supported comparable predator numbers which in turn lead to uniform levels of predation between the forest structures. Improved methodology for my study therefore, would include placing the continuous forest plots at least 150m into the forest interior.

Although the abundance of many interior forest birds is reduced in fragmented landscapes, many of the bird predators of FTC are regularly found in isolated forest stands. For example, the Baltimore oriole (*I. galbula*) (Peterson 1990), American Robin (*Turdus migratorius*) (Drolet *et al.* 1999), brown-headed cowbird (*Molothrus ater*) (Peterson 1990) and the American crow (*Corvus brachyrhynchos*) (Hannon and Coterill 1998) are often associated with, and thrive in, lightly wooded areas, forest edges and forest fragments. These birds, and others exhibiting similar habitat preferences, may increase their use of isolated forest patches and forest edges thereby compensating for

reduced predation by species that preferentially use continuous forest. Predators of FTC found predominantly in forest fragments in this study were the least flycatcher (*Empidonax minimus*), the brown-headed cowbird (*Molothrus ater*) and the chipping sparrow (*Spizella passerine*), none of which are considered forest interior species (Hannon and Schmiegelow 2002; Hobson and Bayne 2000).

Bird-mediated predation of FTC was not only similar between forest structures, but also similar among forest fragments of different sizes, connectedness and distances to continuous forest. The trend of increasing predation with increasing fragment isolation distance, seen in Chapter two, is not related to bird predation. These results suggest that bird predators of FTC use forest fragments equally, regardless of size, isolation distance and connectedness in the landscape. Bayne and Hobson (2001) found that even area-sensitive ovenbirds (*Seiurus aurocapillus*), a known predator of FTC, often uses forest fragments of different sizes. Similarly, yellow warblers (*Dendroica petechia*) have been shown to use multiple patches within their home range (Celada 2000), thereby inflicting similar rates of predation among fragments.

Forest fragmentation and beetle-mediated predation of FTC

Anthropogenic practices affect the distribution and abundance of forest carabid species (Barbaro *et al* 2005; Beaudry *et al.* 1997; Burke and Goulet 1998; Driscoll and Weir 2005; Halme and Niemela 1993; Petit and Usher 1998). Beetle-mediated predation was however, similar between forest structures and among fragments of varying size, connectedness and isolation distance to the continuous forest. These results suggest that beetle predators of FTC pupae are either abundant in both forest structures due to the presence of stable resident populations or, are not impeded by the spatial structure of the landscape.

Both forest edges and small forest fragments may act as ecotones, supporting both forest and field beetle fauna (Martin *et al* 2001). Since continuous forest plots were generally located close to the forest edge and the majority of forest fragments were very small, forest carabid populations within each structure may have been subject to similar

environmental conditions and levels of competition and predation with invading field fauna (Burke and Goulet 1998). Field species and habitat generalists such as *Calosoma monoliatum* and *Pterostichus melanarius*, *Pterostichus adstrictus*, and *Carabus chamissonis* were found in both forest structures indicating conditions were likely comparable and thus supported similar beetle predator communities, which in turn may explain why predation rates did not differ between forest structures. Similarly, Mitchell (2001) found that predation of FTC parasitoid pupae in the soil, was equally intensive in fragments and along continuous forest edges. She found however, that predation by ground foragers was lower in interior forest plots (> 200m from the forest edge). Both our studies suggest that ground predators perceive forest fragments and forest edges as similar habitats.

It was expected that beetle-mediated predation rates would be significantly lower among smaller, poorly connected fragments and among fragments with the greatest isolation distances from the continuous forest because the abundance of forest carabids has been shown to decrease in smaller (less than three hectares), more isolated forest fragments (Burke and Goulet 1998; Halme and Niemela 1993). There were no linear effects of fragment size, connectedness, or the isolation distance, on beetle predation. Many species in the large-bodied genus *Calosoma* are strong fliers, particularly *C. frigidum*, which can disperse over long distances (Crins 1980; Lindroth 1969) and have been shown to rebound quickly after timber harvesting (Beaudry *et al.* 1997). In addition, *P. melanarius*, a common open-habitat species of ground beetle, has been recorded in high abundance in poplar-aspen forests in central Alberta (Niemela and Spence 1991) and can easily disperse over long distances into suitable habitat (Niemela and Spence 1991; Zalewski 2004). It is therefore possible that individuals of *P. melanarius* and those belonging to the genus *Calosoma* can easily migrate to isolated forest stands, resulting in similar predation rates among forest fragments and between forest structures.

There was a non-linear effect of patch size on beetle-mediated predation. As patch size increased from one to two hectares, so too did predation. Above two hectares however, predation decreased. These results are likely an artifact of low sample size; eight out of

the 12 fragments were less than two hectares in area and the similarity in patch sizes may have precluded detection of any linear trends or biologically meaningful nonlinear trends.

Landscape Context

Results of fragmentation and disturbance studies are largely scale-dependent and trends at one spatial scale are not necessarily representative of all spatial scales (e.g. Roland 1993) and that in multi-species systems, the response is likely species-specific (Roland and Taylor 1997). The present study was conducted at one scale which may not have been appropriate for the generalist predators under study. Hobson and Bayne (2000) found that the amount of forest cover within a five kilometre radius affected forest songbird species composition Similarly, Vanbergen *et al.* (2005) found that carabid beetle species composition, richness and abundance were all lower in continuously forested regions than in agricultural and grassland regions measured in 1 km^2 blocks. Burke and Goulet (1998) found that small woodlots with little regional forest cover showed little beetle diversity whereas small woodlots with high amounts of regional forest cover (similar to my study sites) exhibited levels of beetle diversity similar to large woodlots. In the present study, the differences in predator species richness and composition between forest types, at larger scales may also be important in understanding predator-prey interactions in the FTC system. I examined the predation rates by bird and beetle communities at a relatively fine scale that might have missed forest interior species, potential predators of FTC pupae. Predation rates therefore should be reexamined within large (>5km) tracts of continuous forest versus a highly fragmented landscape of the same area. At this larger spatial scale, it is possible that fragmentation has a more noticeable impact on predation rates of FTC pupae, particularly by birds.

Pattern of predation across the range of FTC densities

Using a range of naturally occurring FTC densities as a surrogate for temporal changes in FTC abundance, I assessed density-dependent predation by bird and beetle guilds separately. In Chapter 2, I showed that together, generalist predators cause substantial mortality of FTC pupae at low densities but do not appear to regulate their populations. In the current chapter, I found that the proportion of pupae taken by individual predator

guilds is also inversely density dependent; however, both trends are extremely weak (Fig 3.6 & 3.7). The lack of significant linear and non-linear effects of FTC density on guild-specific predation implies that birds and beetles individually cannot regulate FTC populations. What then, may be maintaining FTC populations low for many generations? Roland and Embree (1995) suggested that winter moth populations are held low by the combined effect of parasitoids and predators. The early- and late-instar parasitoids of FTC, *Aleiodes malacosomatos* (Mason) and *Lespesia frenchii* (Williston), as well as the tachnid parasitoid *Leschenaultia exul* (Townsend), are relatively important mortality agents during early phases of FTC outbreaks (Parry 1994, Witter and Kulman 1979). Similarly, ichneumon wasps are frequently reared from FTC during the beginning of outbreaks (Witter and Kulman 1979). Together, these parasitoids and predators may be able to maintain the prey populations at low levels for extended periods of time. Furthermore, predation of the egg and larval stages of FTC were not examined. Although egg parasitism does not vary with density and does not appear to be important for the regulation of FTC, FTC eggs can be an important source of food for resident birds such as chickadees (Hodson 1941) and they may be able to inflict high rates of mortality. Alternatively, other birds inflict great mortality on larvae and pupae (Parry 1994; Sealy 1980) and thus it is possible, that generalist predators have a differential impact on other developmental stages of FTC, which was not quantified in this study.

Predation may be affected by the location of the deployed pupae within the canopy. Schauber *et al.* (2004) found that predators exhibited a type III functional response in the forest habitat (1.5 meters above ground) whereas predation rates on the forest floor remained high across all densities, suggesting that generalist predators may perceive microhabitats as discrete foraging patches. During innocuous population phases, FTC generally pupate in the upper canopy but during outbreaks, they will pupate anywhere, including the herbaceous layer. In the present study, predation rates were only assessed in the upper shrub/sapling layer, therefore it is possible that beetle predation was underestimated since the predatory beetles may remain in the lower shrub/herbaceous layer where densities of FTC are equally high. Similarly, predation in the upper canopy was not assessed, which may have missed predation by numerous bird species. Parry

(1994) for example, documented orioles foraging most frequently in the upper canopy as opposed to the shrub/sapling layer, thus my estimates of bird predation may have been artificially low. This may have been of particular importance in assessing predation at low density, when most of pupae are in the canopy.

Predator Abundance

Generalist predators are by definition limited in their numerical response to increasing prey density thus it was not surprising that the abundance of bird predators was unaffected by FTC density. Sealy (1980) however, found that the abundance of orioles (*I. galbula*) increased during an outbreak of FTC in Manitoba. The spatial extent of that outbreak was not known and birds may have been responding to small scale, local increases of FTC through movement as well as reproduction. Morris *et al.* (1958) also found that warbler abundance increased during an outbreak of spruce budworm (*Choristoneura fumiferana* Clemens). Other bird species however, did not, suggesting that responses are generally species specific. In my study, the assessment of individual species' responses to FTC density was not possible due to low sample size.

In Chapter two, I found that predation of FTC pupae was lower in the second year of study and I attributed this decrease to lower rates of avian predation. I suggested the decrease in avian-type predation was caused by 1) a reduction in the number of bird predators, or 2) an increase in pupal parasitism rates in the second year, which would in turn decrease avian predation of FTC. In the current study, I determined that bird predators of FTC increased in the second year, suggesting that fluctuations in bird predator abundance have little effect on bird-mediated FTC predation. Parasitism, although not likely the only cause of reduced bird-type predation, appears to be more important in driving avian predation of FTC.

The abundance and spatial distribution of carabid predators of FTC are affected by various factors including; winter conditions, substrate type, predation, and competition (Thiele 1977). Using pitfall traps, I found few beetle predators. At one site however, a high number of *P. melanarius* were trapped from both of the paired forest plots. This site was characterized by a consistently high background density of FTC over the two years

of study, to which beetles may have responded. Although there were a high number of beetles within these paired plots, predation rates of the deployed pupae were relatively low. These results are suggestive of a type II functional response of beetle predators, even though none was found. To assess the impact of beetle predators on FTC populations more thoroughly, beetle-mediated predation rates should also be examined at ground level, rather than only in the shrub layer.

Vegetation complexity

According to the enemies hypothesis (Root 1973), as environments become increasingly complex, the diversity of prey increases; allowing the establishment of a more stable and diverse community of generalist predators. In addition, regulation of prey around a stable equilibrium should be improved with increasing complexity because the environment provides more refuges allowing prey to escape local extinction. In my study, there was no effect of tree diversity on bird-mediated predation of FTC because bird predators are likely more affected by the regional forest composition than the composition at a local scale (Diaz *et al.* 2005). Increased tree diversity negatively affected predation rates of FTC pupae by beetles, but this relationship was weak. Although beetle predators of FTC are generalists, they may be found more frequently in monocultures of aspen which dominated all low diversity sites. For example, the main beetle predator, *C. frigidum,* is most frequently found in deciduous forests (Work *et al.* 2004) and rarely in mixed woods, thus the plots of increased stand diversity, which generally had higher amounts of spruce and pine, may not have supported as many *C. frigidum* individuals.

It was expected that the proportion of the plots covered with herbaceous material (vegetation density) would negatively affect beetle predation rates due to a decreased ability to move as vegetation density increased. There was however, no effect of vegetation density on beetle-mediated predation rates of FTC. It appears that the beetles that prey on FTC pupae in the canopy are not affected by ground vegetation.

Summary

Although predation by *all* predators was shown to have a relatively large effect on FTC populations (Chapter 2), this chapter suggests that individually, birds and beetles have much less of an impact on FTC. Furthermore, these predators showed no evidence of being capable of regulating low density FTC populations, either individually or separately although they both exhibited a weak de-stabilizing pattern rather than a regulating one. Limited sample size may have prevented the detection of density-dependent predation by either predator guild.

Fragmentation appears to have little effect on guild-specific predation rates. Guild-specific predation rates may have been comparable between forest structures due to similarities in the environmental conditions of the paired plots, similarities in bird and beetle predator communities between structures, and good colonization ability of the predators. These results suggest that isolated stands do not act as prey refuges from which outbreaks may arise. In contrast, the creation of habitat edges appears to decouple host-parasitoid interactions, increasing survival of FTC and prolonging outbreaks (Roland 1993). Survival of FTC is also further increased along edges due to decreased virus transmission (Roland and Kaupp 1995) and increased parasitoid predation along edges and within fragments, but not in the forest interior (Mitchell 2001). A comparison of bird-mediated and beetle-mediated predation rates of FTC along edges and within the forest interior may provide better information on whether fragmentation has an effect on predation rates. Because the environments along edges and in small fragments are similar, it may have precluded detection of a fragment effect. Furthermore, fragmentation effects may not be detected at the scale used in this study thus I recommend assessing predation rates at larger spatial scales, as landscape effects are not always detected at one particular scale (e.g. Roland and Taylor 1997).

LITERATURE CITED

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation - a landscape perspective. *Ecology* **73**:794-804.

Aquilani, S. M. and J. S. Brewer. 2004. Area and edge effects on forest songbirds in a non-agricultural upland landscape in northern Mississippi, USA. *Natural Areas Journal* **24**:326-335.

Barbaro, L., L. Pontcharraud, F. Vetillard, D. Guyon, and H. Jactel. 2005. comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. *Ecoscience* **12**:110-121.

Bayne, E. M. and K. A. Hobson. 2001a. Effects of habitat fragmentation on pairing success of ovenbirds: importance of male age and floater behavior. *Auk* **118**:380-388.

Bayne, E. M. and K. A. Hobson. 2001b. Movement patterns of adult male ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. *Condor* **103**:343-351.

Beaudry, S., L. C. Duchesne, and B. Cote. 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Canadian Journal of Forest Research* **27**:2065-2071.

Burke, D. and H. Goulet. 1998. Landscape and area effects on beetle assemblages in Ontario. *Ecography* **21**:472-479.

Burke, D. M. and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* **115**:96-104.

Campbell, R. W. 1975. The gypsy moth and its natural enemies. USDA *Agricultural Information Bulletin* **381**.

Celada, C. 2000. Territory choice and quality in the yellow warbler (*Dendroica petechia*). The importance of habitat spatial structure, spatial scale, social factors and the impact of cattle grazing. PhD dissertation. University of Alberta, Alberta.

Crawford, H. S. and D. T. Jennings. 1989. Predation by birds on spruce budworm *Choristoneura fumiferana* - functional, numerical, and total responses. *Ecology* **70**:152-163.

Crins, W. J. 1980. Aggregations of *Calosoma frigidum* (Coleoptera, Carabidae) in Ontario during 1976. *Entomological News* **91**:155-158.

Desrochers, A. and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* **11**:1204-1210.

Diaz, I. A., J. J. Armesto, S. Reid, K. E. Sieving, and M. F. Willson. 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloe' Island, Chile. *Biological Conservation* **123**:91-101.

Doherty, P. F. and T. C. Grubb. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. *Ecology* **83**:844-857.

Driscoll, D. A. and T. Weir. 2005. Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology* **19**:182-194.

Drolet, B., A. Desrochers, and M. J. Fortin. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *Condor* **101**:699-704.

Elkinton, J. S., A. M. Liebhold, and R. M. Muzika. 2004. Effects of alternative prey on predation by small mammals on gypsy moth pupae. *Population Ecology* **46**:171-178.

Ficken, M. S. and R. W. Ficken. 1966. Notes on mate and habitat selection in yellow warbler. *Wilson Bulletin* **78**:232.

Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* **33**:301-310.

Halme, E. and J. Niemela. 1993. Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici* **30**:17-30.

Hannon, S. J. and S. E. Cotterill. 1998. Nest predation in aspen woodlots in an agricultural area in Alberta: the enemy from within. *Auk* **115**:16-25.

Hannon, S. J. and F. K. A. Schmiegelow. 2002. Corridors may not improve the conservation value of small reserves for most boreal birds. *Ecological Applications* **12**:1457-1468.

Hobson, K. A. and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixed woods of western Canada. *Wilson Bulletin* **112**:373-387.

Hodson, A. C. 1941. An ecological study of the forest tent caterpillar, *Malacosoma disstria* Hbn. *Minnesota Agricultural Experiment Station Technical Bulletin* **148**

Holling, C. S. 1965. The functional response of predators to prey density. *Memoirs of the Entomological Society of Canada* **45**:1-60.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator prey interactions. *Nature* **326**:388-390.

Larochelle, A. 1990. The food of carabid beetles (Colepptera: Carabidae, including cicindelinae). Fabreries Supplement **51**-132.

Lassau, S. A., D. F. Hochuli, G. Cassis, and C. A. M. Reid. 2005. Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions* **11**:73-82.

Lindroth, C. H. 1. 1969. The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Opuscula Entomologica Supplementum. Part 1-6.

Martin, M., F. Bastardie, D. Richard, and F. Burel. 2001. Studying boundary effects on animal movement in heterogeneous landscapes: the case of *Abax ater* (Coleoptera : Carabidae) in hedgerow network landscapes. *Comptes Rendus De L'Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences* **324**:1029-1035.

Mitchell, A.A. 2001. Generalist predation on tachinid parasitoids of the forest tent caterpillar in fragmented landscapes. Masters Thesis. Univeristy of Alberta, Alberta.

Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* **39**:487-494.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* **117**:393-408.

Niemela, J. and J. R. Spence. 1991. Distribution and abundance of an exotic ground-beetle (Carabidae) - a test of community impact. *Oikos* **62**:351-359.

Norton, M. R. and S. J. Hannon. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Canadian Journal of Forest Research* **27**:44-53.

Parry, D. 1994. The impact of predators and parasitoids on natural and experimentally created populations of forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). Masters Thesis, University of Alberta, Alberta.

Pearce, J. L., L. A. Venier, J. Mckee, J. Pedlar, and D. Mckenney. 2003. Influence of habitat and microhabitat on carabid (Coleoptera : Carabidae) assemblages in four stand types. *Canadian Entomologist* **135**:337-357.

Peterson, R.T. 1990. Western Birds. Houghton Mifflin Company. Boston, US.

Petit, S. and M. B. Usher. 1998. Biodiversity in agricultural landscapes: the ground beetle communities of woody uncultivated habitats. *Biodiversity and Conservation* **7**:1549-1561.

Rail, J. F., M. Darveau, A. Desrochers, and J. Huot. 1997. Territorial responses of boreal forest birds to habitat gaps. *Condor* **99**:976-980.

Raymond, B., A. Vanbergen, A. Watt, S. E. Hartley, J. S. Cory, and R. S. Hails. 2002. Escape from pupal predation as a potential cause of outbreaks of the winter moth, *Operophtera brumata*. *Oikos* **98**:219-228.

Robinson, S. K. 1998. Another threat posed by forest fragmentation: reduced food supply. *Auk* **115**:1-3.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* 93:**25**-30.

Roland, J. 1994. After the decline - What maintains low winter moth density after successful biological control? *Journal of Animal Ecology* **63**:392-398.

Roland, J. and D. G. Embree. 1995. Biological control of the winter moth. *Annual Review of Entomology* **40**:475-492.

Roland, J. and W. J. Kaupp. 1995. Reduced transmission of forest tent caterpillar (Lepidoptera, Lasiocampidae) nuclear polyhedrosis virus at the forest edge. *Environmental Entomology* **24**:1175-1178.

Roland, J. and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**:710-713.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats - fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95-120.

Schauber, E. M., R. S. Ostfeld, and C. G. Jones. 2004. Type 3 functional response of mice to gypsy moth pupae: is it stabilizing? *Oikos* **107**:592-602.

Sealy, S. G. 1980. Reproductive responses of northern orioles to a changing food supply. *Canadian Journal of Zoology* **58**:221-227.

Southwood, T. R. E. and H. N. Comins. 1976. Synoptic population model. *Journal of Animal Ecology* **45**:949-965.

Thiele, H.U. 1977. Carabid Beetles in Their Environment. A Study on Habitat Selection by Adaptations in Physiology and Behaviour. Springer-Verlag. Berlin/New York.

Vanbergen, A. J., B. A. Woodcock, A. D. Watt, and J. Niemela. 2005. Effect of land-use heterogeneity on carabid communities at the landscape scale. *Ecography* **28**:3-16.

Villard, M. A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *Auk* **115**:801-805.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**:1211-1214.

Winfree, R., J. Dushoff, E. E. Crone, C. B. Schultz, R. V. Budny, N. M. Williams, and C. Kremen. 2005. Testing simple indices of habitat proximity. *American Naturalist* **165**:707-717.

Witter, J. A., H. M. Kulman. 1972 A review of the parasites and predators of tent caterpillars (*Malacosoma* spp.) in North America. *Minnesota Agriculture Experimental Station Technical Bulletin* **289**.

Witter, J.A., H.M. Kulman. 1979. The parasite complex of the forest tent caterpillar in northern Minnesota. *Environmental Entomology* **8**:723-731

Work, T. T., C. M. Buddle, L. M. Korinus, and J. R. Spence. 2002. Pitfall traps and capture of three taxa of litter-dwelling arthropods: implications for biodiversity studies. *Environmental Entomology* **31**:438-448.

Work, T. T., D. P. Shorthouse, J. R. Spence, W. J. A. Volney, and D. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the ecosystem management emulating natural disturbance (Emend) landbase in northwestern Alberta. *Canadian Journal of Forest Research* **34**:417-430.

Zalewski, M. 2004. Do smaller islands host younger populations? A case study on metapopulations of three carabid species. *Journal of Biogeography* **31**:1139-1148.

Chapter 4

General Conclusions

CONCLUSIONS

To understand the population dynamics of forest tent caterpillars (FTC), the impact of mortality agents must be assessed through the entire cycle. Most studies have focused only on those agents most important during the outbreak and decline phases of the cycle. This is the first study that has attempted to describe the pattern of generalist predation across a broad range of naturally occurring FTC population densities. The goal of this thesis was to assess predation rates of all generalist predators together, as well as identify the impact of bird and beetle guilds separately. Furthermore, the effect of habitat fragmentation on generalist predation was also of interest because fragmentation has previously been found to negatively affect parasitoids (Roland and Taylor 1997), reduce virus transmission (Roland and Kaupp 1997) and decrease parasitoid survival (Mitchell 2001). I addressed these objectives by assessing predation using predator exclusion treatments in paired plots of continuous forest and forest fragments, across a gradient of FTC densities.

General predation

Generalist predators appear to have a moderate (Chapter 2) to low (Chapter 3) impact on populations of forest tent caterpillars. The results suggested however, that the influence of predators on FTC can vary temporally. In Chapter 2, I showed that all generalist predators combined had a greater impact on FTC populations in 2003 than in 2004. I suggested that the decline in predation between years was related to the decreases in avian pupal consumption rates in 2004 (Chapter 3). The proportion taken by beetles however, remained relatively consistent between years (Chapter 3). Furthermore, terrestrial predators and predators accessing FTC from the canopy (assumed to be beetle and bird predators, respectively), act additively in that they depredate pupae at the same rate in the presence or absence of the other predator guild.

Pattern of predation across the range of FTC densities

Predators of FTC exhibit a destabilizing pattern of predation as prey densities change; as prey density increases, predation rates decrease monotonically (Type II functional

response; Holling 1965). This was particularly evident for all predators combined (Chapter 2). Similar results were evident for bird-mediated and beetle-predation rates (Chapter 3) but sample size was low and reduced my ability to detect statistical significance for these patterns (Chapter three).

Birds appear to preferentially consume unparasitized pupae. These results are consistent with the findings by Parry (1994) who found that birds often abandoned parasitized pupae. Beetles on the other hand, did not preferentially select either unparasitized or parasitized pupae (Chapter two). Because FTC parasitism rates were higher in 2004, I suggest that parasitism may have been responsible for the reduction in bird predation in that year since they seem to not prey on parasitized prey. The individual impact of birds and parasitoids, particularly at low density, may be important in maintaining innocuous FTC population levels because they are somewhat mutually exclusive. In contrast, the absence of selectivity by beetles suggests they may be an important source of parasitoid mortality. Mitchell (2001) found that ground foragers, which include predatory beetles, are in fact important predators of parasitoids pupating in the soil but she detected no density dependence in predation rates of these parasitoids.

Forest structure and predation

Overall predation by generalist predators did not differ between fragments and continuous forests (Chapter 2). I suggest that predators were not affected by habitat fragmentation measured at scale at used in this study. This was reflected in that bird predator populations were similar between forest structures (Chapter 3). Beetle predator abundance was not compared between habitat structures due to low sample size, but beetle-mediated predation rates, like those for birds, were similar between forest structures. The ability to detect an effect of fragmentation on predation may be a function of the spatial scale used. Effects of fragmentation on bird and beetle communities may be found only at larger scales, such as 5km (birds: Hobson and Bayne 2000) and 1km (beetles: Vanbergen *et al.* 2005). Therefore, to assess landscape effects more thoroughly, I suggest that predation should be assessed against percent forest cover, at progressively larger scales, as has been done by others (e.g. Roland and Taylor 1997).

Further research

Given that generalist predators alone are not capable of regulating low density populations of FTC, it is possible that they act with other mortality agents of FTC to maintain endemic levels of prey. Some parasitoids appear to be important throughout different phases of low density. For example, *Carcelia malacosomae* (Sellers), *Aleiodes malacosomatos* (Mason), *Lespesia frenchi* (Williston) are suspected of being important parasitoids during low density and early outbreak phases of FTC cycles (Parry 1994; Witter and Kulman 1979), and in conjunction with generalist predators, may be able to maintain low densities over time. Further research examining the interaction between predators and parasitoids during the endemic phase may shed light on the dynamics affecting low density populations.

In this study, I examined only predation of FTC pupae. Predation on other developmental stages may be more important and thus should be assessed. It has been suggested that the setae found on late instar larvae are a deterrent to potential predators; however, many avian predators have been found to rip open the larva and eat the inner contents (Parry 1994; Sealy 1980). Furthermore, many smaller bird species and some beetle species have frequently been reported to eat early-instar larvae and eggs (Hodson 1941; Parry 1994; Sealy 1979; Weed 1899, 1900); thus depredation on these stages should not be ignored. Some developmental stages, namely the late instar stages, migrate between trees, thus entering alternate predator foraging habitats and therefore may be subject to different predation pressures during these times and the shape that this predation takes may change accordingly. As mentioned, predators are selective in terms of the stages of FTC they consume. Since I examined guild-specific rates of predation, rates of predation by individual species were obscured. I therefore suggest that predation by individual predators, rather than guilds, should be examined since predators will likely have differential effects on the numerous developmental stages of FTC. Mitchell (2001) found that shrews were more likely than beetles and other ground predators, to prey on parasitoid pupae suggesting that different predators may play different roles in FTC population dynamics.

LITERATURE CITED

Hobson, K. A. and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixed woods of western Canada. *Wilson Bulletin* **112**:373-387.

Hodson, A. C. 1941. An ecological study of the forest tent caterpillar, *Malacosoma disstria* Hbn. *Minnesota Agricultural Experiment Station Technical* Bulletin **148**

Holling, C. S. 1965. The functional response of predators to prey density. *Memoirs of the Entomological Society of Canada* **45**:1-60.

Mitchell, A.A. 2001. Generalist predation on tachinid parasitoids of the forest tent caterpillar in fragmented landscapes. Masters Thesis. University of Alberta, Alberta.

Parry, D. 1994. The impact of predators and parasitoids on natural and experimentally created populations of forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). Masters Thesis, University of Alberta, Alberta.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* **93**:25-30.

Roland, J. and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**:710-713.

Schmidt, B. C. 2001.Ecology of low-density forest tent caterpillar (*Malacosoma disstria*) populations: pheromone monitoring methodology and the role of parasitoid alternative hosts. Masters Thesis. University of Alberta, Alberta.

Sealy, S. G. 1979. Extralimital nesting of bay-breasted warblers - response to forest tent caterpillars. *Auk* **96**:600-603.

Sealy, S. G. 1980. Reproductive responses of northern orioles to a changing food supply. *Canadian Journal* of *Zoology* **58**:221-227.

Vanbergen, A. J., B. A. Woodcock, A. D. Watt, and J. Niemela. 2005. Effect of land-use heterogeneity on carabid communities at the landscape scale. *Ecography* **28**:3-16.

Weed, C. M. 1900. The forest tent caterpillar. New Hampshire Agricultural Experiment Station Bulletin **75**:107-132.

Weed C, M. 1899. The forest tent caterpillar. New Hampshire College Agricultural experiment Station Bulletin **64**:75-98.

Witter, J.A., H.M. Kulman. 1979. The parasite complex of the forest tent caterpillar in northern Minnesota. *Environmental Entomology* **8**:723-731

APPENDIX A

Appendix A.1. Species list and abundance of bird predators recorded in 2003, at sites located in the Rocky Mountain House Provincial Grazing Reserve region. (Sources: Hodson 1941; Parry 1994; Ramse 1975; Weed 1899; 1900; Witter and Kulman 1972)

Common name	Scientific name	Fragment	Continuous	Abundance
Veery†	*Catharus fuscescens*	0	0	0
Red-winged blackbird‡	*Agelaius phoeniceus*	2	0	2
Northern flicker‡	*Colaptes auratus*	0	0	0
Eastern kingbird‡	*Tyrannus tyrannus*	1	1	2
American crow‡	*Corvus brachyrhynchos*	0	2	2
White-throated sparrow‡	*Zon otrichia albicollis*	0	1	1
Ovenbird†	*Seiurus aurocapillus*	1	2	3
Red-eyed vireo‡	*Vireo olivaceus*	2	2	4
Chipping sparrow‡	*Spizella passerine*	1	2	3
Yellow warbler‡	*Dendroica petechia*	0	0	0
Least flycatcher‡	*Empidonax minimus*	2	1	3
Yellowbellied sapsucker‡	*Sphyrapicus varius*	2	2	4
Warbling vireo†	*Vireo gilvus*	0	0	0
Black-capped chickadee †	*Poecile atricapillus*	1	3	4
Rose-breasted Grosbeak†	*Pheucticus ludovicianus*	1	0	1
Brown-headed cowbird‡	*Molothrus ater*	8	2	10
American robin‡	*Turdus migratorius*	3	3	6
Black and white warbler†	*Mniotilata varia*	1	3	4
House wren‡	*Troglodytes aedon*	1	0	1
Pine siskin†	*Carduelis pinus*	0	0	0
Eastern phoebe‡	*Sayornis phoebe*	1	0	1
Baltimore oriole‡	*Icterus galbula*	1	1	2

† Species identified as forest habitat specialists in Alberta, Canada (Blomme 1991; Hodson 1941; Parry 1994; Pelech and Hannon 1995; Ramse 1975; Sealy 1978; 1980; Weed 1899; 1900; Witter and Kulman 1972)

‡ Species identified as habitat generalists in Alberta, Canada (Hannon and Schmeigelow 2002; Peterson 1990)

Appendix A.2. Species list and abundance of bird predators recorded in 2003, at sites located in the Black Bear. (Sources: Hodson 1941; Parry 1994; Ramse 1975; Weed 1899; 1900; Witter and Kulman 1972)

Common name	Scientific name	Fragment	Continuous	Abundance
Veery†	*Catharus fuscescens*	0	1	1
Red-winged blackbird‡	*Agelaius phoeniceus*	0	0	0
Northern flicker‡	*Colaptes auratus*	0	0	0
Eastern kingbird‡	*Tyrannus tyrannus*	0	2	2
American crow‡	*Corvus brachyrhynchos*	1	1	2
White-throated sparrow‡	*Zon otrichia albicollis*	0	4	4
Ovenbird†	*Seiurus aurocapillus*	1	3	4
Red-eyed vireo‡	*Vireo olivaceus*	3	13	16
Chipping sparrow‡	*Spizella passerine*	0	0	0
Yellow warbler‡	*Dendroica petechia*	1	2	3
Least flycatcher‡	*Empidonax minimus*	8	0	8
Yellowbellied sapsucker‡	*Sphyrapicus varius*	0	0	0
Warbling vireo†	*Vireo gilvus*	0	0	0
Black-capped chickadee †	*Poecile atricapillus*	0	0	0
Rose-breasted Grosbeak†	*Pheucticus ludovicianus*	1	0	1
Brown-headed cowbird‡	*Molothrus ater*	0	0	0
American robin‡	*Turdus migratorius*	0	0	0
Black and white warbler†	*Mniotilata varia*	0	4	4
House wren‡	*Troglodytes aedon*	0	0	0
Pine siskin†	*Carduelis pinus*	0	0	0
Eastern phoebe‡	*Sayornis phoebe*	1	0	0
Baltimore oriole‡	*Icterus galbula*	0	0	0

† Species identified as forest habitat specialists in Alberta, Canada (Blomme 1991; Grant 1959; Hodson 1941; Parry 1994; Pelech and Hannon 1995; Ramse 1975; Sealy 1978; 1980; Weed 1899; 1900; Witter and Kulman 1972)

‡Species identified as habitat generalists in Alberta, Canada (Hannon and Schmeigelow 2002; Peterson 1990)

Appendix A.3. Species list and abundance of bird predators recorded in 2004, at sites located in the Rocky Mountain House Provincial Grazing Reserve region. (Sources: Hodson 1941; Parry 1994; Ramse 1975; Weed 1899; 1900; Witter and Kulman 1972)

Common name	Scientific name	Fragment	Continuous	Abundance
Veery†	*Catharus fuscescens*	2	5	7
Red-winged blackbird‡	*Agelaius phoeniceus*	0	2	2
Northern flicker‡	*Colaptes auratus*	0	0	0
Eastern kingbird‡	*Tyrannus tyrannus*	0	0	0
American crow‡	*Corvus brachyrhynchos*	2	2	4
White-throated sparrow‡	*Zon otrichia albicollis*	3	5	8
Ovenbird†	*Seiurus aurocapillus*	1	13	14
Red-eyed vireo‡	*Vireo olivaceus*	4	10	14
Chipping sparrow‡	*Spizella passerine*	9	7	16
Yellow warbler‡	*Dendroica petechia*	6	7	13
Least flycatcher‡	*Empidonax minimus*	6	2	8
Yellowbellied sapsucker‡	*Sphyrapicus varius*	2	5	7
Warbling vireo†	*Vireo gilvus*	1	1	2
Black-capped chickadee †	*Poecile atricapillus*	1	0	1
Rose-breasted Grosbeak†	*Pheucticus ludovicianus*	3	3	6
Brown-headed cowbird‡	*Molothrus ater*	11	1	12
American robin‡	*Turdus migratorius*	2	1	3
Black and white warbler†	*Mniotilata varia*	0	0	0
House wren‡	*Troglodytes aedon*	6	1	7
Pine siskin†	*Carduelis pinus*	0	4	4
Eastern phoebe‡	*Sayornis phoebe*	0	1	1
Baltimore oriole‡	*Icterus galbula*	2	3	5

† Species identified as forest habitat specialists in Alberta, Canada (Blomme 1991; Grant 1959; Hodson 1941; Parry 1994; Pelech and Hannon 1995; Ramse 1975; Sealy 1978; 1980; Weed 1899; 1900; Witter and Kulman 1972)

‡Species identified as habitat generalists in Alberta, Canada (Hannon and Schmeigelow 2002; Peterson 1990)

Appendix A.4. Species list and abundance of bird predators recorded in 2004, at sites located in the Black Bear Mountain House Provincial Grazing Reserve region. (Sources: Hodson 1941; Parry 1994; Ramse 1975; Weed 1899; 1900; Witter and Kulman 1972)

Common name	Scientific name	Fragment	Continuous	Abundance
Veery†	*Catharus fuscescens*	1	0	1
Red-winged blackbird‡	*Agelaius phoeniceus*	0	0	0
Northern flicker‡	*Colaptes auratus*	1	0	1
Eastern kingbird‡	*Tyrannus tyrannus*	1	0	1
American crow‡	*Corvus brachyrhynchos*	5	5	10
White-throated sparrow‡	*Zon otrichia albicollis*	4	4	8
Ovenbird†	*Seiurus aurocapillus*	3	14	17
Red-eyed vireo‡	*Vireo olivaceus*	15	14	29
Chipping sparrow‡	*Spizella passerine*	9	3	12
Yellow warbler‡	*Dendroica petechia*	2	6	8
Least flycatcher‡	*Empidonax minimus*	7	4	11
Yellowbellied sapsucker‡	*Sphyrapicus varius*	0	3	3
Warbling vireo†	*Vireo gilvus*	0	0	0
Black-capped chickadee †	*Poecile atricapillus*	1	0	1
Rose-breasted Grosbeak†	*Pheucticus ludovicianus*	0	0	0
Brown-headed cowbird‡	*Molothrus ater*	0	0	0
American robin‡	*Turdus migratorius*	1	1	2
Black and white warbler†	*Mniotilata varia*	0	1	1
House wren‡	*Troglodytes aedon*	0	0	0
Pine siskin†	*Carduelis pinus*	0	1	1
Eastern phoebe‡	*Sayornis phoebe*	0	0	0
Baltimore oriole‡	*Icterus galbula*	0	0	0

† Species identified as forest habitat specialists in Alberta, Canada (Blomme 1991; Hodson 1941; Parry 1994; Pelech and Hannon 1995; Ramse 1975; Sealy 1978; 1980; Weed 1899; 1900; Witter and Kulman 1972)

‡Species identified as habitat generalists in Alberta, Canada (Hannon and Schmeigelow 2002; Peterson 1990)

LITERATURE CITED

Blomme, C. G. 1991. Ring-billed gulls, *Larus delawarensis*, feeding in flight on forest tent caterpillar, *Malacosoma disstria*, cocoons. *Canadian Field-Naturalist* **105**:280-281.

Hannon, S. J. and F. K. A. Schmiegelow. 2002. Corridors may not improve the conservation value of small reserves for most boreal birds. *Ecological Applications* **12**:1457-1468.

Hodson, A. C. 1941. An ecological study of the forest tent caterpillar, *Malacosoma disstria* Hbn. *Minnesota Agricultural Experiment Station Technical Bulletin* **148.**

Parry, D. 1994. The impact of predators and parasitoids on natural and experimentally created populations of forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). Masters Thesis, University of Alberta, Alberta.

Pelech, S. and S. J. Hannon. 1995. Impact of tent caterpillar defoliation on the reproductive success of black-capped chickadees. *Condor* **97**:1071-1074.

Peterson, R.T. 1990. Western Birds. Houghton Mifflin Company. Boston, US.

Ramse D.A. Biological control of the forest tent caterpillar, *Malacosoma disstria* Hbn., in North Dakota. Masters Thesis, North Dakota State University, South Dakota.

Sealy, S. G. 1979. Extralimital nesting of bay-breasted warblers - response to forest tent caterpillars. *Auk* **96**:600-603.

Sealy, S. G. 1980. Reproductive responses of northern orioles to a changing food supply. *Canadian Journal* of *Zoology* **58**:221-227.

Weed, C. M. 1900. The forest tent caterpillar. New Hampshire College *Agricultural Experiment Station Bulletin* **75**:107-132.

Weed C., M. 1899. The forest tent caterpillar. New Hampshire College *Agricultural experiment Station Bulletin* **64**:75-98.

Witter, J. A., H. M. Kulman. 1972 A review of the parasites and predators of tent caterpillars (*Malacosoma* spp.) in North America. *Minnesota Agriculture Experimental Station Technical Bulletin* **289**.

APPENDIX B: The abundance of beetle predators of FTC pupae in continuous forest plots and forest fragments in both study regions in 2004

Scientific Name	**Continuous** Rocky	**Continuous** Black Bear	**Fragment** Rocky	**Fragment** Black Bear	**Abundance**
Calosoma frigidum	2	9	3	8	22
Calosoma monoliatum	1	0	3	0	4
Calosoma calidum	0	2	0	1	3
Pterostichus melanarius	54	1	35	0	90
Carabus taedatus	1	0	2	0	3